

Late Ordovician-Early Silurian trace fossils from the Matapedia Group, Tobique River, western New Brunswick, Canada.

II. Additional discoveries with descriptions and comments

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Previous recordings of Late Ordovician-Early Silurian flysch trace fossils (13 ichnogenera, 15 ichnospecies) from slope deposits of the Matapedia Basin at a single site on the Tobique River, western New Brunswick, are supplemented by the addition of 9 newly discovered ichnogenera (12 ichnospecies). These are: *Circulichnis montanus*, *Cruziana problematica*, *Cruziana cf. stromnessa*, *Diplichnites* ichnosp., *Megagraption irregulare*, *Monocraterion* ichnosp., *Phycosiphon incertum*, *Rusophycus didymus*, *Rusophycus* ichnospp. types A and B, *Scolicia* ichnosp. and *Tuberculichnus* ichnosp. The traces are poorly preserved and occur only in low numbers compared to previously documented forms. Nevertheless, the meticulous sampling procedures adopted at the site emphasize the need for detailed collecting, before drawing conclusions regarding diversity models, stratigraphic distribution, etc., of trace fossils. Of these new forms only *Diplichnites* ichnosp. has previously been recorded from the Matapedia Basin in the partially coeval Lower Silurian Siegas Formation. *Tuberculichnus* ichnosp. is recorded for the first time in North America. The combined total of 22 ichnogenera (27 ichnospecies) from the Tobique River represents the most diverse ichnocoenosis yet reported from a single ancient slope deposit. The occurrence of several more typically shallow-water ichnogenera (e.g., *Cruziana*, *Diplichnites*, *Monocraterion* and *Rusophycus*) suggests that, at least in the Early Palaeozoic, caution must be exercised in their utilization as distinctive facies or environmental indicators.

9 nouveaux ichnogenres (12 ichnoespèces) s'ajoutent à ceux déjà répertoriés (13 ichnogenres, 15 ichnoespèces) en un site unique localisé sur la rivière Tobique, dans l'ouest du Nouveau-Brunswick, dans des sédiments tardiordoviciens à éosiluriens accumulés sur le talus continental du Bassin de Matapedia. Ce sont: *Circulichnis montanus*, *Cruziana problematica*, *Cruziana cf. stromnessa*, *Diplichnites* ichnosp., *Megagraption irregulare*, *Monocraterion* ichnosp., *Phycosiphon incertum*, *Rusophycus didymus*, *Rusophycus* ichnospp. types A et B, *Scolicia* ichnosp. et *Tuberculichnus* ichnosp. Ces dernières sont mal conservées et relativement rares par rapport aux formes déjà connues. Néanmoins, le dépouillement méticuleux utilisé à ce site démontre la nécessité d'une collecte détaillée avant de tirer des conclusions quant aux modèles de diversité, à la distribution stratigraphique, etc., des traces fossiles. De ces nouvelles formes, seule *Diplichnites* ichnosp. est déjà connue dans le Bassin de Matapedia, soit dans la Formation silurienne inférieure et en partie synchrone de Siegas. On recense *Tuberculichnus* ichnosp. pour la première fois en Amérique du Nord. Le total combiné de 22 ichnogenres (27 ichnoespèces) présents sur la rivière Tobique représente l'ichnocoenose la plus diverse jamais répertoriée dans un seul dépôt de talus. La présence de plusieurs ichnogenres typiques d'une faible tranche d'eau (e.g., *Cruziana*, *Diplichnites*, *Monocraterion* et *Rusophycus*) démontre que la prudence est de mise lors de leur utilisation à titre d'indicateurs de faciès ou de milieu, tout particulièrement à l'Eopaléozoïque.

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INTRODUCTION

In a recent publication (Pickerill *et al.*, 1987) we documented a relatively diverse Late Ordovician-Early Silurian flysch

ichnocoenosis from slope deposits of the Matapedia Group on the Tobique River, western New Brunswick. In that publication we described 13 ichnogenera (15 ichnospecies) from a single site (Fig. 1), noting that the entire assemblage represented the most

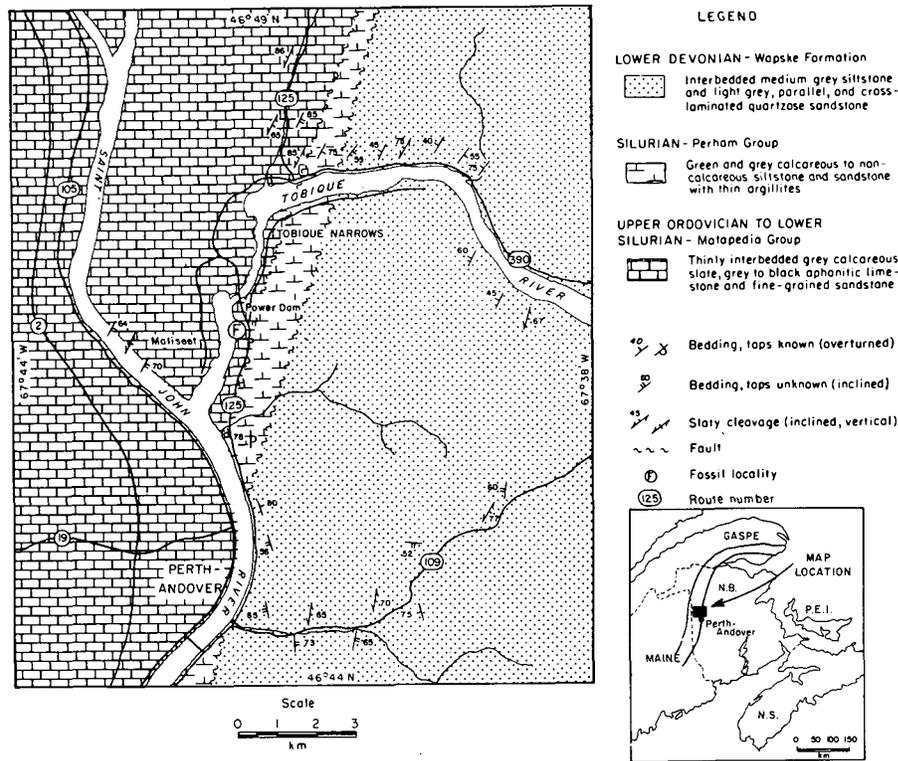


Fig. 1. Location and simplified geological map of the Perth-Andover area, western New Brunswick. In the small inset map the Matapedia Basin is outlined by a stippled ornament.

diverse ichnocoenosis formally recorded from Lower Palaeozoic slope deposits. As previously reported, the site (Fig. 1) is situated on the planned location of a trout and salmon aquaculture centre. This construction has now been initiated and its eventual completion will result in coverage of many of the exposed strata and removal of the associated and considerable talus deposits from which most of the trace fossils were collected.

In view of its ichnological importance, the New Brunswick Department of Natural Resources and Energy provided a minority group summer contract to Donna and Regina Pearly, who for three months systematically collected, sorted (under supervision) and donated the material from the site to us for further study. The vast amount of productive material yielded many further examples of all the previously reported ichnogenera (see Pickerill *et al.*, 1987, and comments, discussion and conclusions section herein). More importantly, it revealed an additional 9 ichnogenera (12 ichnospecies) not previously discovered by us. The purpose of this paper is therefore to document, particularly systematically, these previously unreported ichnogenera and, as a corollary, to briefly comment on the importance and relevance of these discoveries with respect to several facets of ichnological research.

SYSTEMATIC PALICHOLOGY

As in our previous paper (Pickerill *et al.*, 1987) we describe the trace fossils in alphabetical order rather than in any formal morphological or behavioural groupings. For brevity, extensive discussion on particular ichnospecies has been minimized and

only pertinent observations, conclusions and/or additional relevant literature have been included. Cleavage formation, pressure solution activity and, presumably, primary compaction of the trace fossils at the Tobique site have effected considerable deformation of most specimens but size measurements have not been corrected for concomitant strain. Additionally, metamorphism has contributed to their generally poor preservation and photographic reproducibility. All figured material has therefore been prepared employing one or, more commonly, a combination of the following methods:- (a) immersion in dilute (10%) hydrofluoric acid for 1-2 minutes, (b) whitening with sublimate of ammonium chloride or (c) enhancement with removable marker ink. All figured material is currently housed in the Department of Geology, University of New Brunswick. Once ichnological studies of the Matapedia Group has been completed, the material will be housed with the Geological Survey of Canada in Ottawa.

Ichnogenus Circulichnis Vialov, 1971

Circulichnis montanus Vialov, 1971 (Fig. 2a)

Description

Seven specimens, poorly preserved in convex hyporelief on siltstone soles or concave or convex epirelief on upper surfaces. Each trace consists of a circular or elliptical burrow, locally collapsed, with a structureless fill identical in grain size to

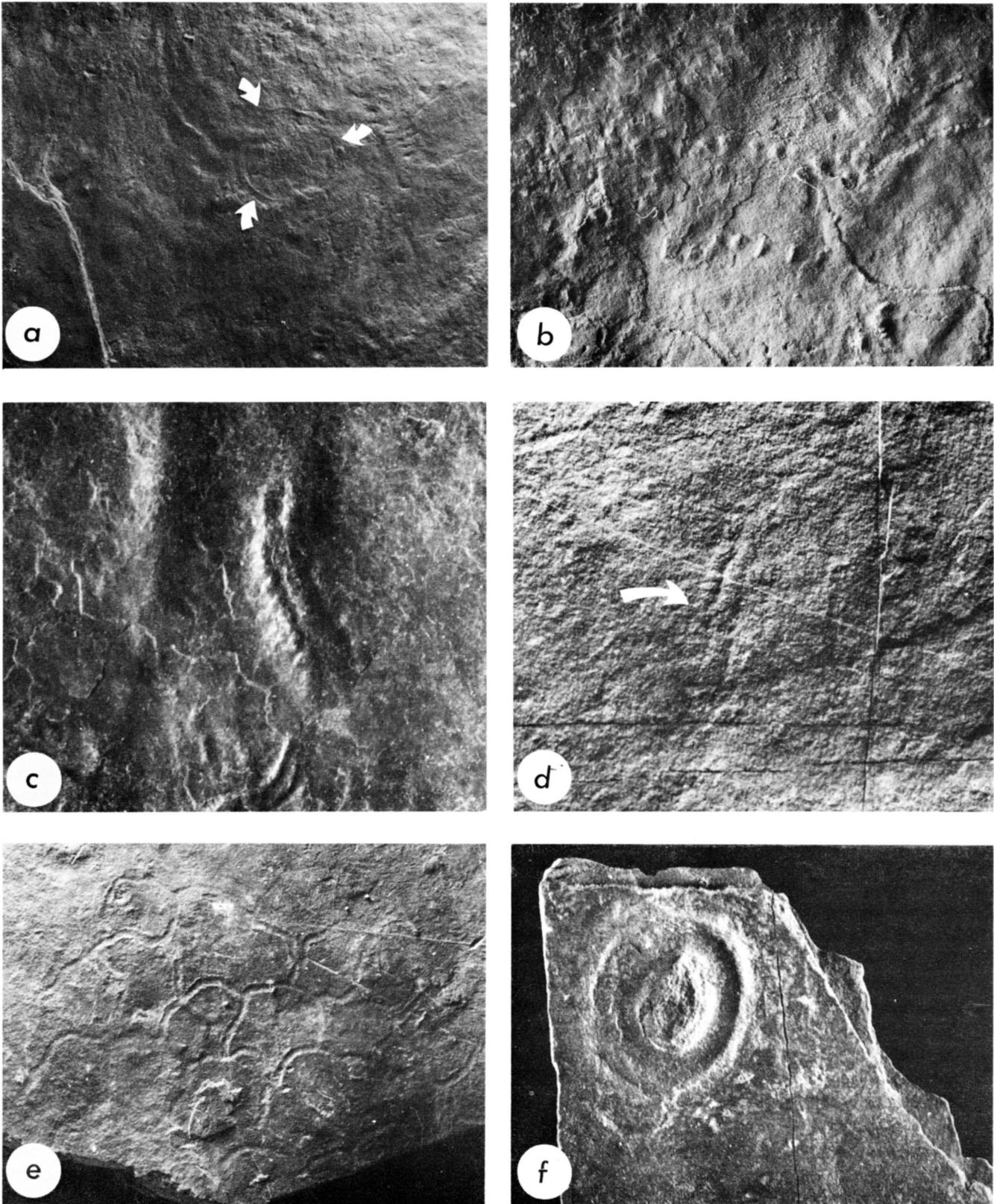


Fig. 2. a. *Circulichnis montanus* (arrowed) preserved in convex hyporelief, x1.0. b. *Diplichnites* ichnosp. preserved in convex hyporelief. Track runs approximately E-W, x1.3. c. *Cruziana* cf. *stromnessa* preserved in convex hyporelief, x3.1. d. *Cruziana problematica* (arrowed) preserved in convex hyporelief, x2.0. e. *Megagraption irregulare* preserved in concave epirelief, x0.6. f. *Monocraterion* ichnosp. funnel preserved in convex epirelief, x1.6.

enclosing sediment. Largest burrow system is 1.9 cm in width with burrow diameter of 1.9 mm; smallest is 0.9 cm in width with burrow diameter of 0.8 mm. Individual burrows are elliptical in cross-section due to compaction.

Remarks

Detailed remarks with respect to the origin and stratigraphic range of *Circulichnis* have been made by Fillion and Pickerill (1984, in press a). Although a eurybathic form, it has more often been reported from deep-water flysch. Its recording from the Tobique site represents the first from the Matapedia Basin of Fyffe *et al.* (1981), though because of its simple morphology we anticipate further discoveries from elsewhere in the basin.

Ichnogenus *Cruziana* d'Orbigny, 1842

Cruziana problematica (Schindewolf, 1921)
(Fig. 2d)

Description

Single, poorly preserved, 20 mm long, curved bilobate sole trace. Lobes are not deeply impressed; each is 2 mm wide with a narrow (<0.5 mm wide) groove separating them along the length of the trace. Each lobe possesses faint scratch marks; each approximately 1 mm apart, oriented normal to the trace axis and crossing the entire lobe.

Cruziana cf. stromnessa (Trewin, 1976)
(Fig. 2c)

Description

Single, 15 mm long, 4 mm wide curved bilobate sole trace, relatively deeply impressed. Each 2 mm wide lobe is separated by a narrow (<0.5 mm wide) groove and possesses dot-like scratch marks, each approximately 1 mm apart, oriented at an angle of 60-80° to the trace axis and crossing the entire lobe.

Remarks

Both specimens are relatively small and narrow compared with more typical examples of *Cruziana* and are more akin to what many previous, and indeed present, authors have referred to as *Isopodichnus* Bornemann, 1889. However, we agree with the reasoning of Bromley and Asgaard (1979) to include *Isopodichnus* within *Cruziana* as realistically the only essential differences between these ichnogenera are, morphologically, in accessory features (*sensu* Fürsich, 1974), which should be employed only for classification at the ichnospecific level. One specimen can clearly be diagnosed as *C. problematica*, which is characterized by being less than 7 mm in width and possessing transverse striations (see Fillion and Pickerill, in press a). The second cannot be confidently assigned to a distinct ichnospecies but closely resembles and hence is compared to *C. stromnessa* as described by Trewin (1976). Additionally, this latter specimen

is virtually identical to the unnamed trace fossil figured by Dahmer (1934, plate 8, fig. 10) from the Early Devonian of southern Germany). Although both *C. problematica* and *C. stromnessa* have previously been recorded from a variety of non-marine and shallow-marine Palaeozoic sequences (see Fillion and Pickerill, in press a), to our knowledge they have never previously been reported from deep-water slope sequences.

Ichnogenus *Diplichnites* Dawson, 1873

Diplichnites ichnosp.
(Fig. 2b)

Description

Simple, straight to gently curved trackways preserved in convex hyporelief on siltstone soles. Each track consists of two parallel series of equally spaced and approximately equal-sized smooth, regular and straight imprints; individual imprints are elongate, 2-3 mm in length and 1 mm or less in width, with their long axes oriented at an angle of approximately 40° to the track axis. Individual track sets (*sensu* Osgood, 1970) are up to 2 cm in maximum (and total) width and 6 cm in maximum observed length.

Remarks

Diplichnites is a morphologically simple trackway but restudy of its 'forms', 'types' and ichnospecies of various authors (e.g., Osgood, 1970; Osgood and Drennen, 1975; Fillion and Pickerill, in press a) is still deemed necessary for any meaningful ichnospecific assignment. It is morphologically similar to *Dimorphichnus* Seilacher, 1955, an arthropod track previously reported by us (Pickerill *et al.*, 1987) from the Tobique site, but differs by possessing approximately equal-sized (length) imprints on each side of the track. Though more typically previously reported from shallow-water marine sequences it has also previously been reported from deep-water strata (e.g., Pickerill, 1981). The recording herein is its first from the Matapedia Group.

Ichnogenus *Megagraption* Książkiewicz, 1968

Megagraption irregulare Książkiewicz, 1968
(Fig. 2e)

Description

Single specimen, poorly preserved in concave epirelief on the upper surface of a thinly-bedded slate. The specimen covers an area of 10 x 8 cm² and consists of an irregular network of variably shaped and sized, but typically relatively large, nets of interconnected polygonal (4-8 sides) ?burrow segments. Individual segments are consistently 2 mm wide, with slightly elevated and well-defined external margins differentiated by colour rather than any difference in grain size. Branching between individual polygons is characteristically at irregular

intervals and at approximately right angles, though because of the shape of individual segments (straight, curved or slightly sinusoidal) these angles vary from 40° to 90°.

Remarks

Megagraption is a distinctive graphoglyptid trace fossil (Seilacher, 1977a). Graphoglyptids are almost universally preserved as positive features in convex hyporelief on bedding plane soles, though rare exceptions have been reported (e.g., Seilacher, 1977a). This particular example therefore represents a unique and fortuitous example of chance preservation. Additionally, it also demonstrates that at least some graphoglyptids were either open burrows prior to casting (cf. Seilacher, 1977a) or, in fact, represent surface traces. Irrespective of origin, the trace can be clearly assigned to *M. irregulare*, which is characterized by its irregularly shaped polygonal nets of different size and common right angle branches at irregular intervals (Książkiewicz, 1977). Although the closely related graphoglyptid ichnogenus *Paleodictyon* Meneghini, 1850 has previously been reported from strata (Grog Brook Group) of the Matapedia Basin (Pickerill, 1980, 1987), *Megagraption*, until now, has never been recorded. The ichnogenus is a typical deep-water form.

Ichnogenus *Monocraterion* Torell, 1870

Monocraterion ichnosp.
(Fig. 2f)

Description

Five specimens, each preserved as a series of spherically or sub-spherically arranged laminae on upper and lower surfaces of thinly-bedded calcareous fine-grained siltstones. On upper surfaces the overall diameter of the essentially circular structures may attain a maximum of 20 mm and on lower surfaces the diameter of the corresponding trace is considerably reduced; thus, individual specimens consist of a funnel-like arrangement of laminae. Whether the funnels are concordant or discordant with respect to the laminae (terminology of Crimes *et al.*, 1977) cannot be ascertained due to the thin nature of the siltstone slabs; however, vertical sections clearly indicate sediment disturbance and downward tapering. The thin slabs also precluded any observation of associated vertical pipe structures which, ideally, but not universally (see Fillion and Pickerill, in press b), should extend downward from the funnels. Funnel depth is at least 7 mm in one example but preservation is typically incomplete.

Remarks

Although incompletely preserved, the downward tapering of the funnels distinguishes the specimens from the morphologically similar trace fossils (when observed only in planes parallel to stratification) *Cylindrichnus* Howard, 1966 and *Laevicyclus* Quenstedt, 1879. The ichnogenus *Rosselia* Dahmer, 1937 also exhibits a similar morphology in plane section but is character-

ized by a central pipe penetrating the funnel. Because of the generally poor and incomplete preservation of the Matapedia material it is only identified at the ichnogenus level. Although Clausen and Vilhjálmsson (1986) recently suggested that *Monocraterion* should be regarded as a junior synonym of *Skolithos* Haldeman, 1840, we follow the recommendation of Fillion and Pickerill (in press b) to retain the ichnogenus (see also Crimes *et al.*, 1977). Though commonly and more typically reported from neritic sequences, *Monocraterion* has also been previously reported from deep-water environments by, for example, Jordan (1981) and MacDonald (1982).

Ichnogenus *Phycosiphon* Fisher-Ooster, 1858

Phycosiphon incertum Fisher-Ooster, 1858
(Fig. 3a)

Description

Horizontal, small U-shaped looped burrows that connect to adjacent U-shaped loops to give the trace an overall antler-like appearance. Burrow diameter is 1-2 mm, consistent within individual systems; loop length variable, up to 9 mm but typically 4-7 mm. Burrow fill is finer grained and is darker in colour than the enclosing fine-grained siltstone. Individual loops do not possess a spreite between their arms.

Remarks

Although lacking a spreite, the material can confidently be assigned to *P. incertum*. Indeed, the majority of figured examples of *P. incertum* (e.g., Häntzschel, 1975, Chaplin, 1980; Marintsch and Finks, 1982, Bjerstedt, 1987) similarly do not possess a spreite. The recording of *P. incertum* from the Matapedia Group at Tobique represents the first from the Matapedia Basin. Although a eurybathic form, the trace is more commonly reported from deep-water flysch sequences.

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus didymus (Salter, 1856)
(Fig. 3b)

Description

Four specimens, preserved in convex hyporelief on the sole of a fine-grained siltstone/shale bed. Each consists of a poorly preserved and only slightly elongate, bilobed, shallow impression, 4-5 mm in total maximum width and 4-6 mm in length, individual lobes being separated by a narrow (<1 mm) but distinct furrow which runs the entire length of the lobes. Individual lobes are parallel and generally smooth, though one specimen displays a hint of very fine transverse striations on one lobe. The four specimens all exhibit a similar orientation suggestive of reotaxis and are associated with miscellaneous and unidentified arthropod markings.

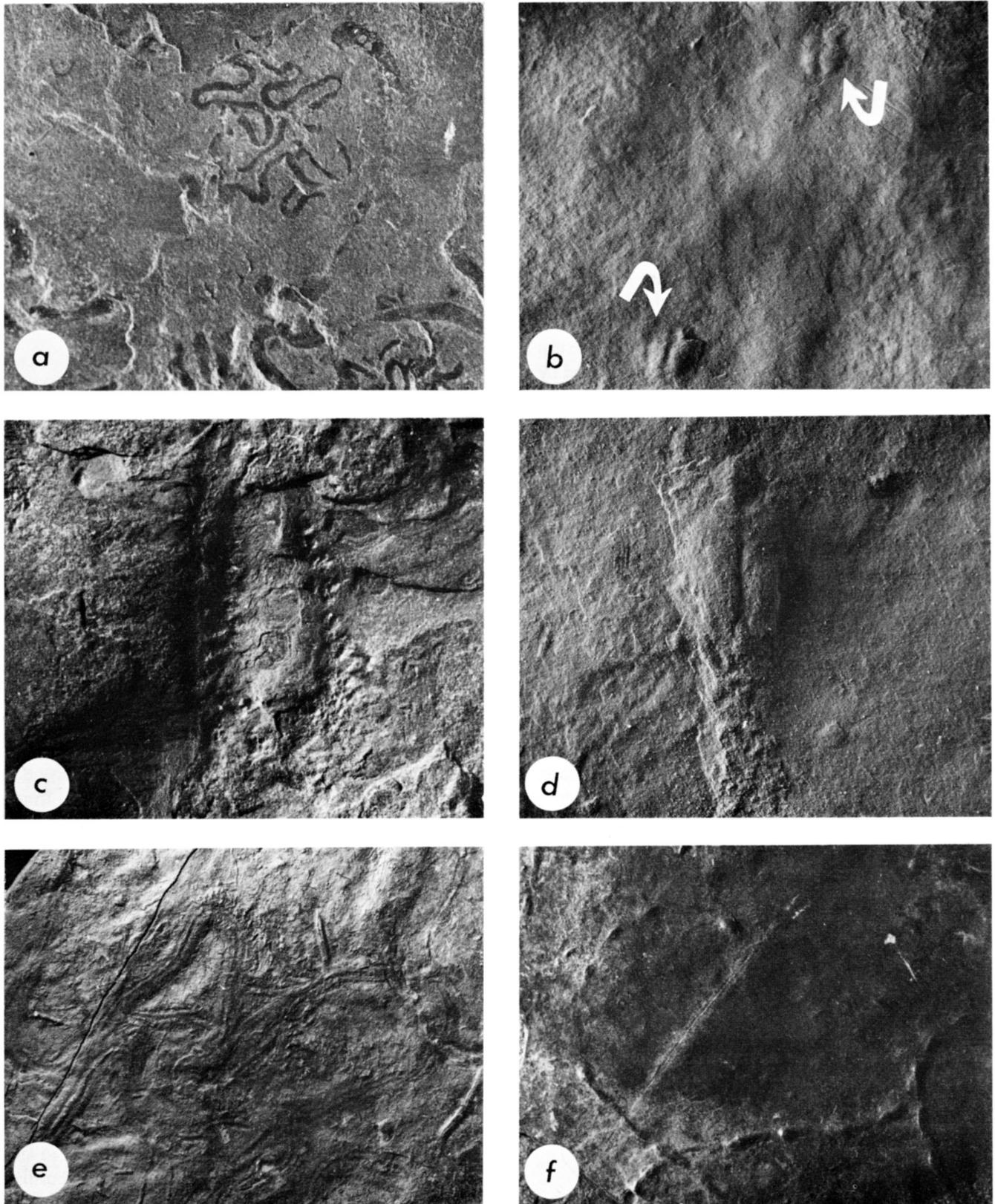


Fig. 3. a. *Phycosiphon incertum* preserved in epirelief on an upper bedding plane surface, x2.0. b. *Rusophycus didymus* (arrowed) preserved in convex hyporelief, x1.5. c. *Rusophycus* ichnosp. type A preserved in convex hyporelief, x1.4. d. *Rusophycus* ichnosp. type B preserved in convex hyporelief, x1.6. e. *Scolicia* ichnosp. preserved in convex hyporelief, x0.6. f. *Tuberculichnus* ichnosp. preserved in convex hyporelief, x1.0.

***Rusophycus* ichnosp. type A**
(Fig. 3c)

Description

One specimen, poorly preserved in convex hyporelief on the sole of a fine-grained siltstone layer. The specimen is very shallowly impressed, bilobed, but posteriorly tapering, 2.5 cm in preserved length, and 1.7 cm in maximum width towards the anterior extremity. Individual lobes are only observed towards their external margins; thus, no central furrow as such can be observed though the sediment is more depressed where the furrow would have existed had preservation been better. The lobes possess crudely developed and irregularly spaced ridges oriented normal to the external margins of the lobes themselves.

***Rusophycus* ichnosp. type B**
(Fig. 3d)

Description

Single specimen, preserved in convex hyporelief on the sole of a coarse-grained siltstone slab. The trace consists of a bilobed elongate impression, 15 mm long, 8 mm in maximum width and slightly tapering posteriorly. Lobes are smooth, moderately impressed and separated by a clearly defined, narrow (<1 mm) median furrow. A small 3 mm long enigmatic ridge protrudes from the anterior end of the central furrow.

Remarks

Of the six specimens of *Rusophycus* identified from the material, four can be confidently assigned to *R. didymus*, which in all probability is the resting impression made by the same arthropod responsible for the production of *Cruziana problematica*. Because of their poor preservation the two other specimens can only be identified at the ichnogenetic level; however, they are clearly different from *R. didymus* and differ from each other. Thus, they are herein described simply as *Rusophycus* ichnosp. type A and *Rusophycus* ichnosp. type B. The latter ichnospecies somewhat resembles *R. pudicum*, particularly with respect to its overall shape, but this may be a preservational artefact. *R. didymus* has previously been reported from non-marine and shallow-marine environments (e.g., Seilacher, 1955; Pickerill and Forbes, 1979) but, to our knowledge, never from a deep-water marine slope sequence.

Ichnogenus *Scolicia* de Quatrefages, 1849

***Scolicia* ichnosp.**
(Fig. 3e)

Description

Two samples, preserved in convex hyporelief on the soles of thinly interbedded siltstone and slate. Each trace consists of a bilaterally symmetrical, irregularly meandering, 7 mm wide

marking consisting of two well-defined lobes, each 3 mm wide, separated by a 1 mm wide ridge, which periodically changes into a furrow and then back into a ridge at irregular intervals along the length of the trace. Lobes are typically smooth but in places possess delicate and closely spaced transverse striations, which cut across the entire lobe surface. External margins of the lobes are clearly defined, and in some places are characterized by slightly elevated and thin marginal ridges, though these are not developed along the whole course of the trace.

Remarks

The ichnogenus *Scolicia* is a morphologically variable and complex form with many preservational variants and is clearly in need of serious and monographic taxonomic revision (Howard and Frey, 1984). Even the material described herein exhibits morphological change within a single trace. For these reasons the material is only identified at the ichnogenetic level and the reader is referred to Chamberlain (1971), Książkiewicz (1977) and Smith and Crimes (1983) for more extensive discussions on the nature, origin and morphological variations of the traces. The recording of the facies-crossing trace fossil *Scolicia* is its first from the Matapedia Basin.

Ichnogenus *Tuberculichnus* Książkiewicz, 1977

***Tuberculichnus* ichnosp.**
(Fig. 3f)

Description

Six specimens, each consisting of irregularly shaped and different sized ridges, pods or tubercles of sediment preserved as positive features in convex hyporelief on the soles of fine-grained sandstones. The pods or tubercles tend to be elongate, up to 8 mm in length and 5 mm in width and are arranged in freely winding, loosely meandering or spiralled rows, individual pods being separated by intervals of undisturbed sediment which vary in length from 1-9 mm. Individual pods are smooth and fill is identical in grain size to enclosing sediment.

Remarks

Książkiewicz (1977) erected three ichnospecies of *Tuberculichnus*, namely *T. vagans*, *T. meandrinus* and *T. bulbosus*, from the Mesozoic flysch of the Polish Carpathians. The diagnoses, descriptions and variations exhibited by each of these are, unfortunately, incomplete but were apparently based on "...the shape and alignment of tubercles..." (Książkiewicz, 1977, p. 140). The ichnospecies *T. vagans* and *T. meandrinus* exhibit considerable overlap with respect to these parameters and a re-study of Książkiewicz's material seems necessary. For this reason the material described herein is only identified at the ichnogenetic level. Książkiewicz (1977) interpreted *T. vagans* as a full burrow and this seems likely for our own material, the distinctive pods simply representing interface portions of a vertically- and horizontally-meandering burrow system similar to that recently

described by Crimes and Anderson (1985) for *Hormosiroidea canadensis*. The recording of *Tuberculichnus* from the Matapedia Group represents its first outside of the Polish Carpathians.

COMMENTS, DISCUSSION AND CONCLUSIONS

The described specimens numerically represent an extremely low proportion of the collected material (<5%), and can generally be regarded as rare forms. Given the industrious sampling procedures, their presence is significant in several respects.

First, their discovery emphasizes the necessity of thorough and detailed sampling procedures (cf. Pickerill, 1980) at single fossiliferous sites, before conclusions are made regarding diversity, stratigraphic distribution, etc., of the various taxa. Indeed, the 9 ichnogenera (12 ichnospecies) reported herein (*Circulichnis*, *Cruziana*, *Diplichnites*, *Megagraption*, *Monocraterion*, *Phycosiphon*, *Rusophycus*, *Scolicia* and *Tuberculichnus*) represent a considerable addition to the 13 ichnogenera (15 ichnospecies) previously reported from the same site by Pickerill *et al.* (1987) (*Cochlichnus*, *Dictyodora*, *Dimorphichnus*, *Glockerichnus*, *Gordia*, *Helminthopsis*, *Muensteria* (= *Taenidium*), *Neonereites*, *Nereites*, *Palaeophycus*, *Syncoprulus* and *Yakutatia*). These latter ichnogenera are all present in the new material and in approximately the same proportions as previously documented (see Pickerill *et al.*, 1987). No additional comments on this material are considered necessary, except perhaps to note that a single slab exhibited gregarious *Yakutatia emersoni*, never previously noted with respect to this ichnospecies.

Second, of these 9 newly discovered ichnogenera, none have been previously reported from the Matapedia Group of the Matapedia Basin of Fyffe *et al.* (1981), although *Diplichnites* has been previously described from coeval strata of the Siegas Formation of the same basin by Pickerill (1981). The other major older and partially coeval stratigraphic unit of the Matapedia Basin, the Grog Brook Group of St. Peter (1977), although itself relatively diverse with respect to trace fossil ichnogenera (see Pickerill, 1987), also contains none of the presently described forms.

Third, of these 9 ichnogenera, only *Megagraption* is a typical deep-water form. *Circulichnis*, *Phycosiphon*, and *Scolicia* are facies-crossing ichnotaxa, while *Tuberculichnus* has only previously been recorded in the flysch of the Polish Carpathians (Książkiewicz, 1977) and therefore further comment is not warranted. Yet *Cruziana*, *Diplichnites*, *Monocraterion* and *Rusophycus* are typical shallow-water forms. Of these latter forms, rare occurrences of *Diplichnites* and *Monocraterion* have previously been noted in deep-water strata (see systematic ichnology), but to our knowledge *Cruziana* and *Rusophycus* have only previously been recorded from non-marine and shallow marine sequences (see also Crimes, 1977). The occurrence of more typically shallow-water ichnotaxa in deep-water flysch of the Matapedia Group somewhat recalls the reverse situation recently reported by Crimes and Anderson (1985) from the Upper Precambrian-Lower Cambrian Chapel Island and Random formations of southeastern Newfoundland. These authors reported several more typical deep-water ichnotaxa (including *Helminthoida*, *Paleodictyon*, *Protopaleodictyon* and *Squamod-*

ictyon) from shallow subtidal strata occurring in association with many more typically shallow-water ichnotaxa. It appears likely, therefore, that in the Early Palaeozoic similar ichnotaxa could be produced in different environments so that most should be regarded as facies-crossing; thus, extreme caution must be exercised in utilizing such ichnotaxa as facies or environmental indicators. Studies on the types and evolutionary development of trace fossils in deep-water Lower Palaeozoic flysch sequences are currently under investigation by one of us (R.K.P.).

Fourth, the additional 9 ichnogenera now extend the overall diversity of ichnotaxa at the Tobique site to 22 ichnogenera (27 ichnospecies). We have already previously commented on the fact that this site preserves the most diverse slope ichnocoenosis reported to date and the additional ichnogenera reported herein further reinforce this conclusion. It seems likely that the Phanerozoic trace fossil diversity models of Seilacher (1974, 1977b) and Frey and Seilacher (1980), which predict diversities of 4-8 ichnospecies for Ordovician and Silurian flysch, are in need of serious revision. Rather, it is our experience that deep-sea trace fossil diversities in Ordovician and Silurian strata may show a broad range (cf. Benton, 1982a). Thus, for example, Benton (1982a,b) records 3 and 20 ichnospecies from, respectively, the Ordovician of East Germany and the Ordovician and Silurian of Scotland; Seilacher (1974) records 4 ichnospecies from the Ordovician of Iraq and the Silurian of Australia and 8 ichnospecies from the Ordovician of Portugal and the Silurian of Wales; Pickerill (1981, 1987) records 16 ichnospecies and ichnogenera from, respectively, Silurian and Ordovician flysch deposits of New Brunswick and Pickerill and Harland (in press) record 9 ichnospecies from flysch slope deposits of the Silurian of northern Greenland (see also Pickerill *et al.*, 1987). Unpublished studies by one of us (R.K.P.) on other Lower Palaeozoic flysch sequences exhibit ichnogenetic diversities of 18 (Cambrian-Ordovician Meguma Group of Nova Scotia) and 19 (Lower Ordovician Levis Formation of Quebec).

Kitchell *et al.* (1978) have demonstrated that diversity of biogenic structures in Recent deep-sea environments can vary considerably, the major influence being the presence or absence of surface-grazing organisms rather than depth or nutrient supply *per se*. Despite the fact that their observations were made primarily on surface-produced structures and they had no means of sampling the infaunal graphoglyptids of Seilacher (1977a), their conclusions do provide a cautionary note that even in the Recent, deep-sea diversities can be varied. Thus, it is likely that a true picture of Early Palaeozoic deep-sea trace fossil diversity cannot be obtained simply by plotting totals for various flysch formations (Benton, 1982a) and that the real patterns are masked by sampling biases and local environmental and preservational factors.

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