

Phycodes templus isp. nov. from the Lower Devonian of northwestern New Brunswick, eastern Canada

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Phycodes templus isp. nov. is described from siliciclastic turbidites of the Wapske Formation of the Tobique Group (Lower Devonian) of northwestern New Brunswick, eastern Canada. The new ichnospecies is characterized by a minimum of two, more typically several, bundled sets of essentially horizontal, broomlike or flabellate, internally structureless, lined burrows. Burrow sets within an individual specimen are interconnected by a single tunnel to form an overall inverted pagoda-shaped structure. The ichnotaxon is believed to have been produced by a vagile deposit feeder, most likely a worm-like organism.

Phycodes templus isp. nov. est décrit à partir d'échantillons provenant de turbidites siliciclastiques de la Formation de Wapske du Groupe de Tobique (Dévonien inférieur) du nord-ouest du Nouveau-Brunswick, dans l'Est du Canada. La nouvelle espèce d'ichnofossile est caractérisée par un minimum de deux, plus typiquement plusieurs ensembles groupés de terriers doublés, essentiellement horizontaux, en forme de balai ou d'éventail et sans structures internes. Les ensembles de terriers dans un spécimen donné sont interconnectés par un tunnel simple pour former une structure d'ensemble en forme de pagode inversée. On croit que l'ichnofossile a été produit par un animal mobile se nourrissant de dépôts et ressemblant probablement à un ver.

[Traduit par la rédaction]

INTRODUCTION

Phycodes Richter, 1850 is a relatively common and widely reported ichnotaxon from Phanerozoic shallow and, less commonly, deep-marine and non-marine environments. The ichnogenus is characterized by essentially horizontal bundled structures of typically flabellate or broomlike burrows that are developed from a single or a few initial (or proximal) tunnels. Such proximal tunnels may or may not possess a spreite. Existing ichnospecies of *Phycodes* are distinguished largely on the nature, style, disposition and degree of burrowing from the initial proximal structures. Ichnological analysis of the Lower Devonian Wapske Formation, northwestern New Brunswick, eastern Canada, has revealed a quite different style of burrowing to that present in existing ichnospecies of *Phycodes*. The purpose of this short contribution is, therefore, to describe this material and, in doing so, to formulate a new ichnospecies, *Phycodes templus*.

LOCATION, STRATIGRAPHY AND GEOLOGICAL SETTING

Specimens described herein are from the Lower Devonian (Helderbergian) Wapske Formation of the Tobique Group of the Riley Brook-Nictau area of northwestern New Brunswick, eastern Canada (Fig. 1). The Wapske Formation, approximately 6 to 9 km thick, is the uppermost formation of the conformably overlying, and partly laterally equivalent, basal Costigan Mountain Formation, approximately 3 km thick, of the Tobique Group (St. Peter, 1978; Dostal *et al.*, 1989). In the Riley Brook-Nictau area, the Wapske Formation consists of an essentially siliciclastic

sedimentary sequence interbedded with decreased proportions of volcanic strata. Pickerill (1986, 1991) and Wilson (1990) have interpreted the depositional environment as deep-marine in origin.

Siliciclastic strata comprise thinly bedded (2-6 cm) and medium bedded (8-20 cm, commonly 4-8 cm) grey, greenish-grey, brown or maroon siltstones and fine-grained sandstones interbedded with 1 to 5 cm thick (commonly 2 cm) shales or mudstones. Studies of coeval strata to the southwest of the Riley Brook-Nictau area (St. Peter, 1978, 1979; Pickerill, 1986; Wilson, 1990) suggest that the Wapske Formation is a relatively deep-water turbiditic sequence deposited below storm wave base. Siltstones and fine-grained sandstones exposed in the Riley Brook-Nictau area commonly show partial Bouma sequences, particularly Tb, Tb-c and Tb-d, and therefore a similar palaeoenvironmental interpretation is not unreasonable.

The material described herein was collected from four roadcut sections along Route 385 that runs parallel to the Mamozekel River, just southwest and northeast of the confluence of the Serpentine River logging road and Route 385 (Fig. 1). At these locations, associated ichnotaxa include *Arthraria* Billings, *Bergaueria* Prantl, *Chondrites* von Sternberg, *Helminthopsis* Heer, *Neonereites* Seilacher, *Palaeophycus* Hall, *Phycodes* Richter, *Rusophycus* Hall, and *Uchirites* Macsotay.

SYSTEMATIC ICNOLOGY

Ichnogenus *Phycodes* Richter, 1850

Type ichnospecies: *Phycodes circinatus* Richter, 1853 by subsequent monotypy.

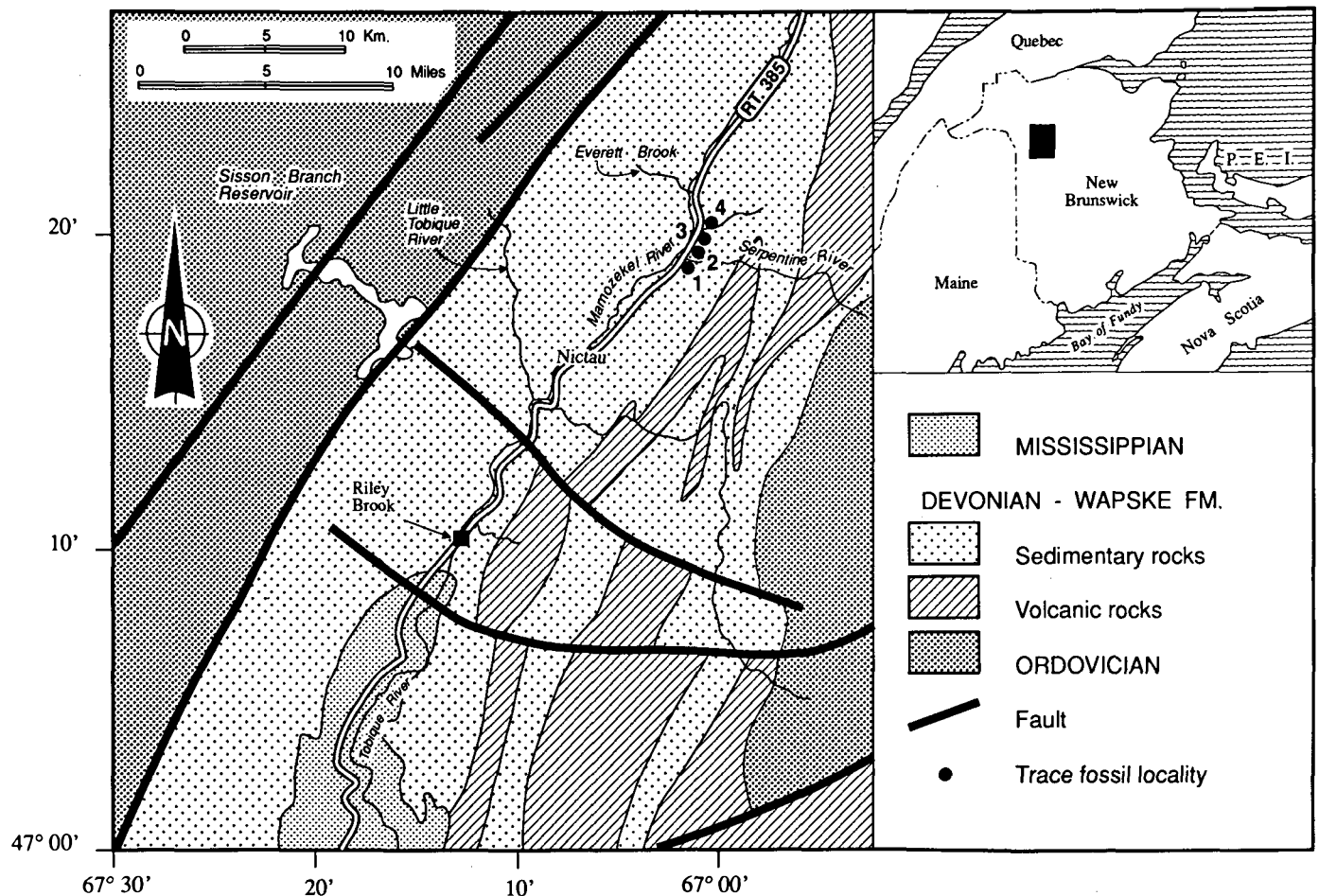


Fig. 1. Simplified geological map of the Riley Brook-Nictau area of northwestern New Brunswick, indicating locations of collected specimens of *Phycodes templus*.

Diagnosis: Horizontally bundled burrows preserved outwardly as convex hyporeliefs. Overall pattern reniform, fasciculate, flabellate, broomlike, ungulate, linear, falcate or circular. Most forms consist of a single or a few main branches showing a spreite-like structure that give rise distally to numerous free branches. In other forms the spreiten are lacking and branching tends to be secund or more random. Individual branches are terete and finely annulate or smooth (after Osgood, 1970; Fillion and Pickerill, 1990).

Discussion: Richter (1850) established *Phycodes* and later (Richter, 1853) erected *P. circinnatum*, which is now regarded as the nomenclatural type of the ichnogenus by subsequent monotypy. There has been considerable confusion regarding the correct spelling of the type ichnospecies of *Phycodes* since Mägdefrau (1934) attempted to revise the original orthographic error made by Richter (1853) by simply modifying the name to *P. circinatum*. Mägdefrau (1934) regarded *Phycodes* as neuter. However, as ichnogenetic names ending in *-odes* must be considered masculine (ICZN, Article 30b), the correct spelling of this ichnospecies is *Phycodes circinatus*. A more detailed discussion on the orthographic history of *P. circinatus* is given in Fillion and Pickerill (1990).

Phycodes has been extensively discussed by Mägdefrau (1934), Seilacher (1955), Osgood (1970), Bradley (1980, 1981) and Fillion and Pickerill (1990). The structure was originally

regarded as a "fucoid" (plant) or an "inorganic structure" (Richter, 1850). However, more detailed studies by these and other authors have shown conclusively that it represents a branching burrow system. The producer has been considered to be a sediment-feeding vermiform annelid (Seilacher, 1955; Häntzschel, 1975), a Pennatulacean (Bradley, 1980), or anthoptiloid sea pen (Bradley, 1981).

Ethologically, two explanations for the origin of the structure have been proposed. Seilacher (1955) considered *Phycodes* a fodinichnion produced by an organism systematically mining a nutrient-rich layer along a silt-mud interface. He proposed that the producing-animal first burrowed down through silt, then moved horizontally in a manner producing a "U"-shaped structure in which one limb was steeper than the other. Following this, the organism withdrew from the distal portion of the burrow and proceeded to excavate a new tunnel adjacent to the previously formed one. Periodically the unbranched proximal portion of the burrow was elevated by removing sediment from the ceiling and packing it, along with waste material, on the floor. This activity gave rise to a retrusive spreite-like structure. When a given area was mined out, a new "master" tunnel was formed at a separate location, and the entire process repeated again. Alternatively, however, Marintsch and Finks (1982) suggested that *Phycodes* may have been formed by an organism that burrowed outwards from a single point and then withdrew to a "home base" only to re-burrow outwards again, following

in part the previously excavated tunnel perhaps as a guide. After complete divergence, the organism subsequently returned to "home base" in order to once again repeat the cycle.

Unlike the suggestion of Seilacher (1955), the material described herein does not possess spreiten in the unbranched proximal burrows. We therefore infer that elevation of these proximal portions was not an active process. Like the suggestion of Marintsch and Finks (1982), however, we believe that in *P. templus* burrowing was initiated from a "home base" followed by withdrawal and then by thigmotaxic horizontal burrowing. Subsequently, however, the producing organism moved forward to establish an interconnected but new "home base" or "master" tunnel to repeat a similar burrowing process. Ethologically, therefore, our material appears to reflect elements of both Seilacher's (1955) and Marintsch and Finks' (1982) explanations. Clearly, a variety of behavioural activities may well be responsible for the production of *Phycodes* and individual examples (and ichnospecies) must be assessed accordingly.

Historically, *Phycodes* was believed to be a reliable indicator of shallow water marine conditions and a characteristic trace fossil of the *Cruziana* ichnofacies of Seilacher (1964), occurring in low-energy environments with relatively stable substrates. However, more recently it has since been reported from non-marine (Pollard, 1985; Buatois and Mángano, 1990), brackish (Hakes, 1985; Greb and Chesnut, 1992) and deep water (Crimes *et al.*, 1977, 1981; Bradley, 1981; Narbonne, 1984; this study) deposits. It ranges in age from Cambrian (Crimes and Anderson, 1985) to Miocene (Bradley, 1981).

Phycodes templus isp. nov.

Figures 2 to 4

? Trail of unknown affinity; Rodriguez and Gutschick, 1970, page 436, plate 10, figure c.

Type material: Holotype NBMG 9202 (Fig. 2A); paratypes NBMG 9203-NBMG 9209 (Figs. 2B, C; 3A-E; 4A-C).

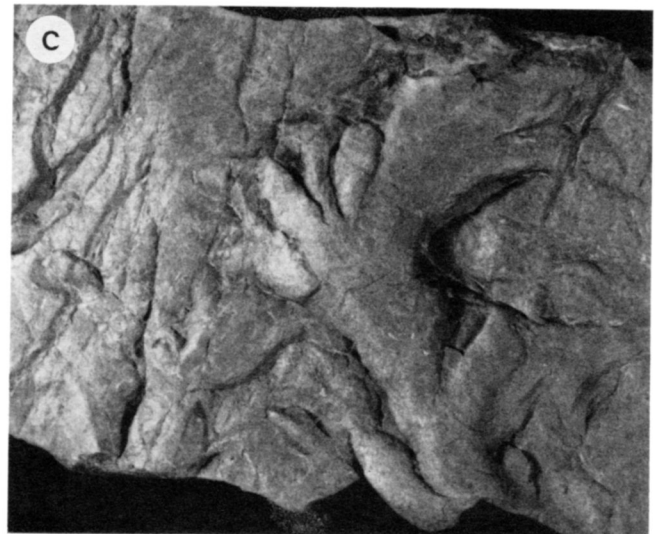
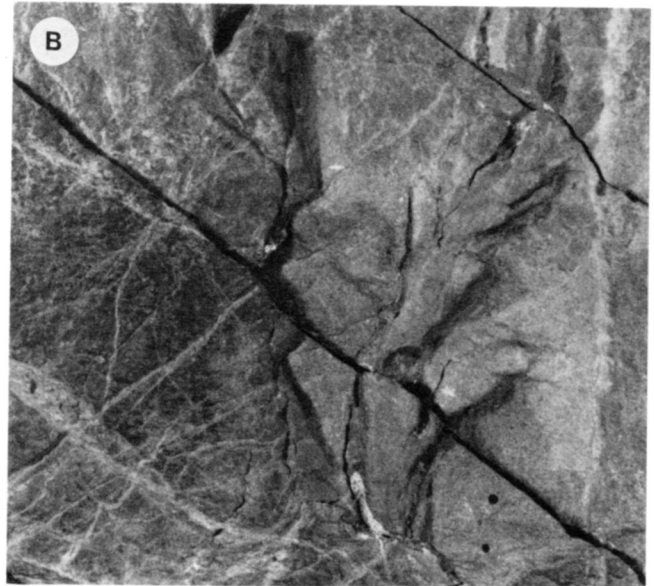
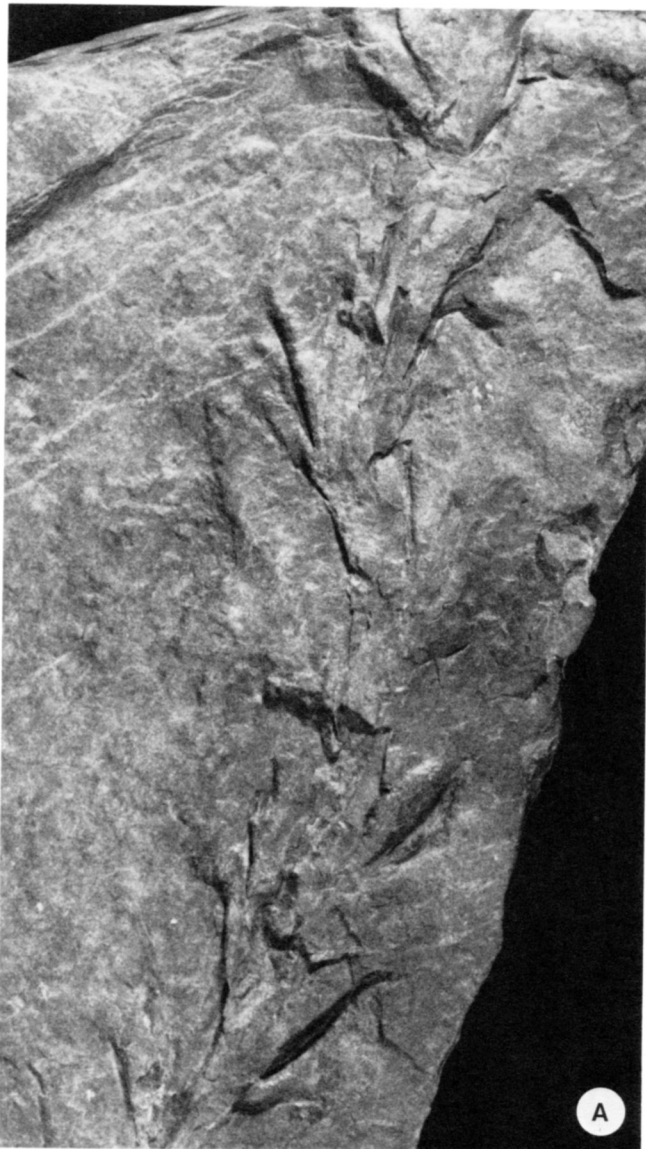


Fig. 2. (A) Holotype of *P. templus*, NBMG 9202, x 0.94. (B) Paratype NBMG 9205, x 0.72. (C) Paratype NBMG 9204, x 0.86, also enlarged in Figure 3C. Preservation is in convex hyporclief.

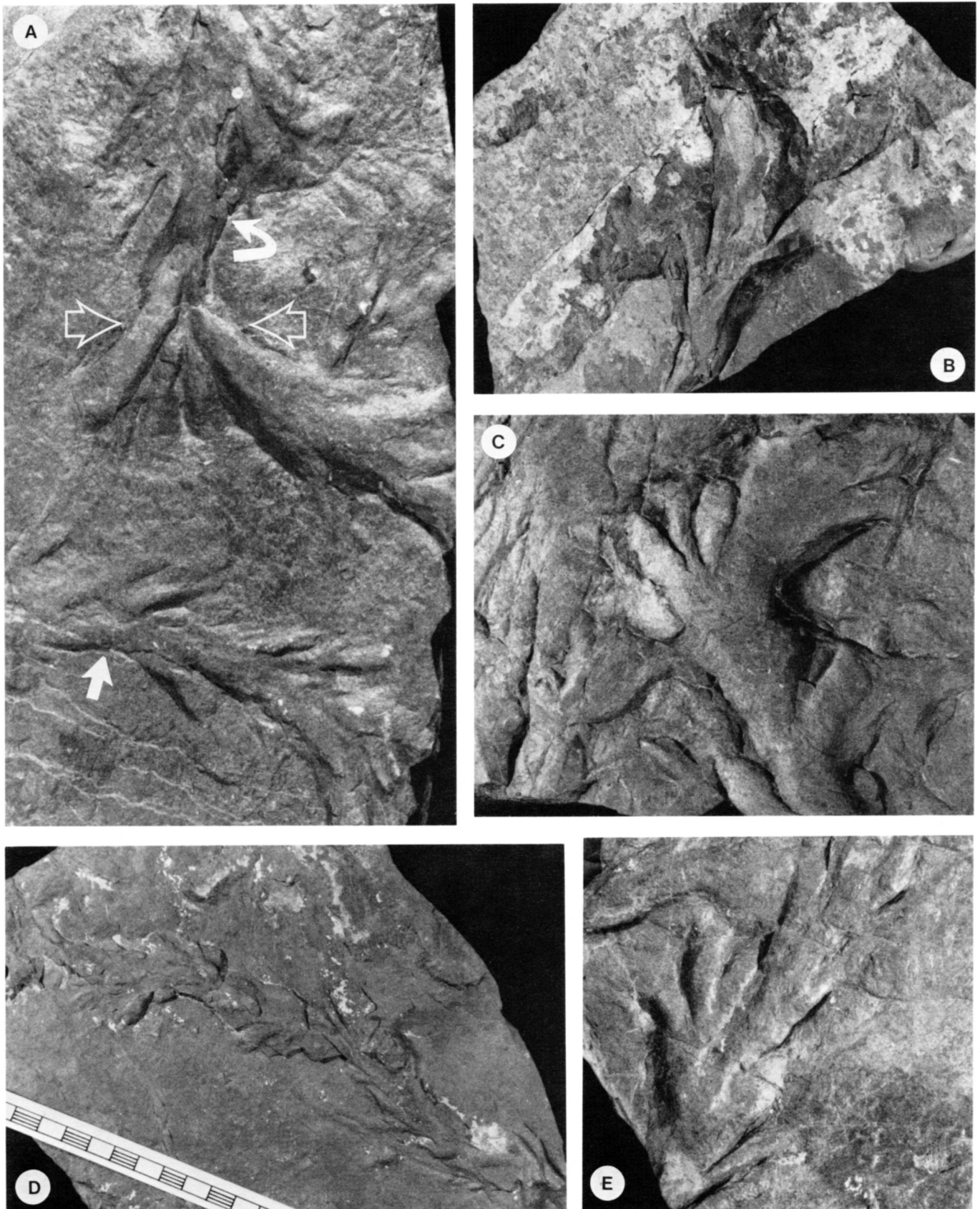


Fig. 3. Paratypes of *P. templus*. (A) Paratypes NBMG 9206, x 1.17 (curved solid arrow) and NBMG 9207, x 1.17 (short solid arrow). Open arrows indicate position of vertical section through NBMG 9206 as illustrated in Figure 4A and C. (B) Paratype NBMG 9203, x 0.76. (C) Paratype NBMG 9204, x 1.06 (see also Fig. 3C). (D) Paratype NBMG 9209, centimetre scale. (E) Paratype NBMG 9208, x 0.81. Preservation of all material is in convex hyporelief.

Material: 13 specimens collected, 8 deposited in the Division of Natural Sciences, Saint John Museum, New Brunswick, Canada, with repository numbers NBMG 9202 - NBMG 9209 inclusive; remaining material located in collections in the Department of Geology, University of New Brunswick.

Etymology: *Templum* (Latin equivalent of pagoda) reflecting the inverted pagoda-like appearance of individual structures.

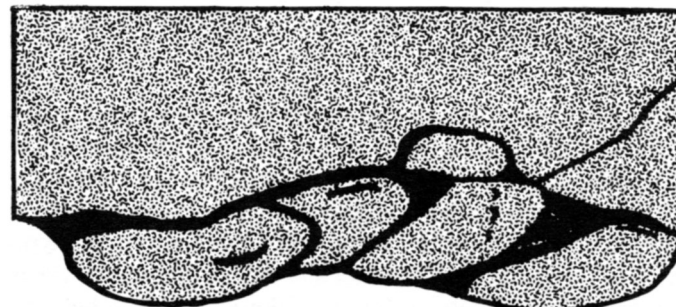
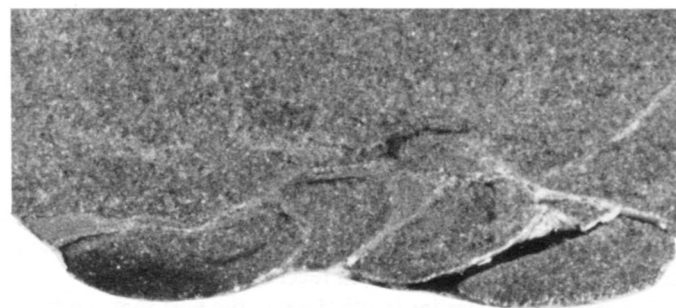
Location: Roadcuts on Route 385, 22 to 26 km northeast of the village of Riley Brook, Victoria County, northwestern New Brunswick, Canada (Fig. 1). NBMG 9204, Location 1, Lat. 47°18.4'N, Long. 67°2.4'W; NBMG 9202 - NBMG 9203, Location 2, Lat. 47°19.7'N, Long. 67°1.8'W; NBMG 9205 - NBMG 9207, Location 3, Lat. 47°19.8'N, Long. 67°1.6'W; NBMG 9208 - NBMG 9209, Location 4, Lat. 47°20.2'N, Long. 67°1.4'W.

Age: The Wapske Formation of the Tobique Group is regarded as Helderbergian (Early Devonian) in age (St. Peter, 1978, 1979; Wilson, 1990).

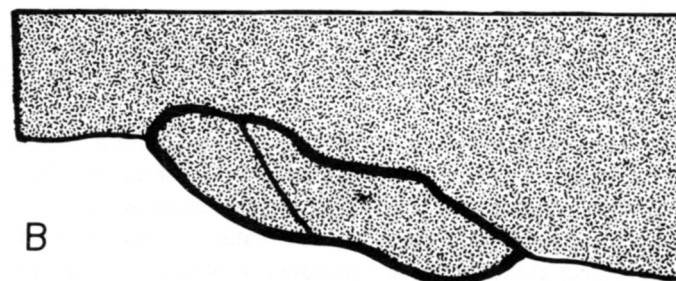
Diagnosis: *Phycodes* possessing two or, more typically, several horizontally interconnected broomlike or flabellate bundles that collectively form an inverted pagoda-like structure.

Description: Specimens are preserved as convex hyporelief expressions of endorelief burrow systems on the soles of 26 to 53 mm thick, grey, argillaceous, micaceous, parallel-laminated siltstone and fine-grained sandstone. Single specimens possess a minimum of 2, typically more (up to 5), sets of broomlike or flabellate bundles of burrows, individual bundle sets each interconnecting horizontally, either straightly (e.g., Fig. 2A) or obliquely (e.g., Fig. 3A), and collectively forming inverted pagoda-shaped structures.

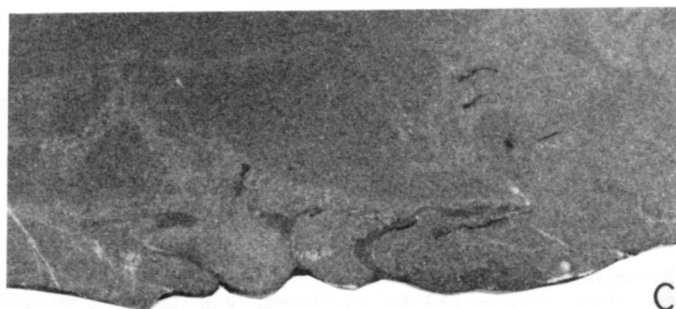
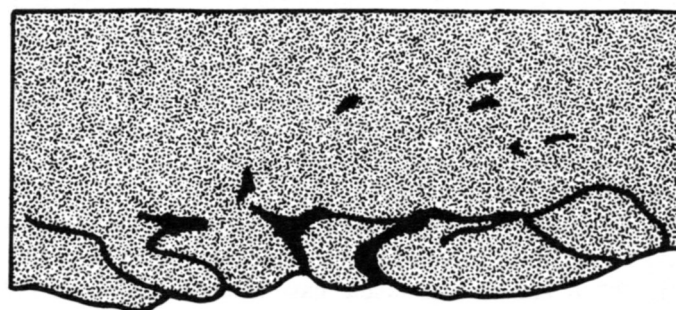
Single broomlike or flabellate bundle sets, each 16 to 45 mm wide, consist of 3 to 7 burrows that are individually essentially straight, more rarely slightly curved, and smooth or covered with delicate wartlike structures. Vertical sectioning of selected sets indicates that individual burrows within a set are typically not vertically tiered to any great extent (Fig. 4). Instead, each set comprises variably elliptical burrows that were apparently only produced, along a single sand-mud interface, but at slightly different levels, and were clearly post-depositional in origin. The primary cross-sectional shape of the individual burrows is difficult to ascertain as a result of primary compaction and subsequent deformation. Individual burrows within a single set are 3 to 9 mm wide and 12 to 45 mm long, burrow width typically increasing distally. Single burrows within



A



B



C

Fig. 4. (A) Vertical section and accompanying sketch of paratype NBMG 9206 of *P. templus* illustrating elliptical lined burrows that do not exhibit well-developed vertical tiers. This view is taken looking directly above the open arrows indicated in Figure 3A, $\times 3.65$. (B) Vertical sketch of the presumed initial proximal burrow of paratype NBMG 9204 of *P. templus*, as illustrated in Figures 2C and 3C, exhibiting well-developed mudstone lining, $\times 4.3$. (C) Vertical section and accompanying sketch of paratype NBMG 9206 of *P. templus* directly below the open arrows indicated in Figure 3A, $\times 2.01$.

a set may or may not vary in length and width. Burrows in individual sets initiate at a single point of origin, subsequent sets initiating from the distal end of a single burrow of the previously established set. Individual sets may or, more commonly, may not overlap. In some instances individual burrows within a single set may bifurcate, although this is uncommon. Typically, interconnected sets occur on the same surface; however, in one example the individual sets, although interconnected, are clearly on a slightly different level of stratification.

Burrow fill is similar in lithology to the host rock, perhaps with a slightly increased mudstone component; individual burrows are bound by an extremely thin (< 0.5 mm), dark mudstone lining (Fig. 4). No spreiten or other internal structures are present.

Remarks: The closely spaced tunnel systems arranged in discrete sets differentiate *Phycodes templus* from the superficially similar ichnogenus *Chondrites* von Sternberg, the latter being characterized by generally systematically branching, commonly dendritic systems, within which individual burrows are typically of much narrower diameter and considerably more widely spaced. The ichnotaxa *Dendrotichnium* Häntzschel and *Dendrorhaphe* Seilacher also exhibit multiple branches from a single stem, but in both, the branches are not arranged in sets and the overall form of the burrow system markedly differs from the material described herein (see Häntzschel, 1975; Seilacher, 1977). Thus, the burrows described herein can clearly be assigned to *Phycodes*.

To our knowledge, 15 additional ichnospecies of *Phycodes* have been named and, or, described in the literature. These ichnospecies were individually distinguished utilizing such characteristics as overall pattern and size, nature, style, disposition and degree of branching and presence or absence of a spreite. Alphabetically, these ichnospecies are: *P.?* *antecedens* Webby, 1970; *P. auduni* Dam, 1990; *P. bromleyi* Dam, 1990; *P. circinatus* Richter, 1853; *P. coronatum* Crimes and Anderson, 1985; *P. curvipalmatum* Pollard, 1981; *P. flabellus* (Miller and Dyer, 1878); *P. gregarius* Chiplonkar and Badve, 1969; *P. harlani* (Hall, 1843); *P.?* *initium* Webby, 1970; *P. palmatus* (Hall, 1852); *P. pedum* Seilacher, 1955; *P. reniforme* Hofmann, 1979; *P. unguatus* Fillion and Pickerill, 1990; and *P. wabanaensis* Fillion and Pickerill, 1990 (Fig. 5).

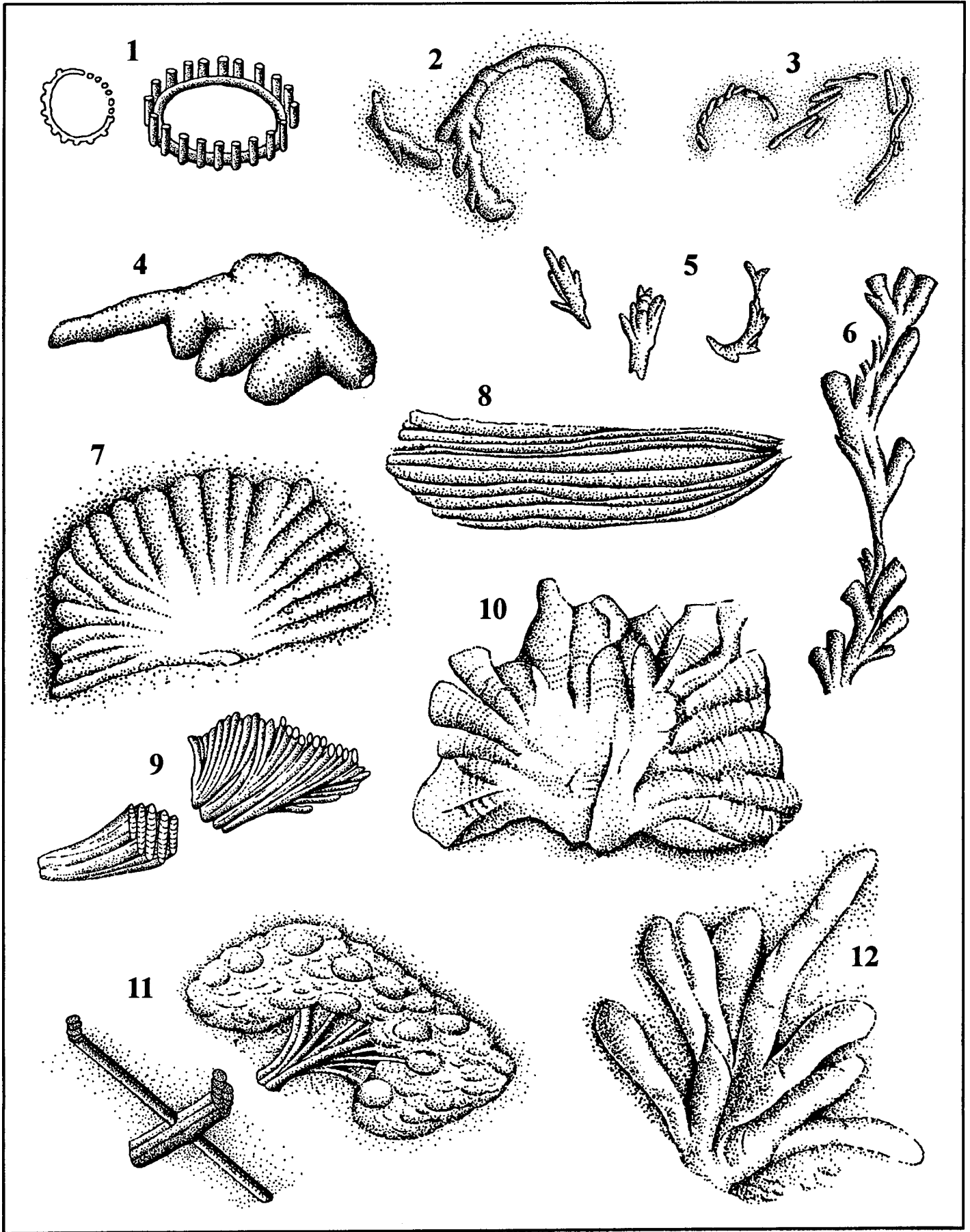
Of these, *P.?* *initium* Webby, 1970 is a *nomen nudum*, having been utilized only in a plate caption (Webby, 1970, p. 102, fig. 20, A and B) that should have actually referred to *P.?*

antecedens as described in the main text of his paper. Apart from the presence on *P.?* *antecedens* of oblique grooves on the primary burrow adjacent to each side branch, we do note that it is otherwise virtually morphologically identical to and could be considered a preservational variant and hence a junior synonym of *P. pedum*. Additionally, *P. gregarius* Chiplonkar and Badve, 1969, being described as *Phycocodes gregarius*, is a *lapsus calami*. As this ichnospecies was formulated from a single specimen and differentiated as such merely on the basis of its small size, it is best regarded as a *nomen dubium* (cf. Pickerill, 1994). Although the quality of the figure is extremely poor, it appears to most closely resemble *P. circinatus*.

We also note that there is still confusion taxonomically with respect to three additional ichnospecies, namely *P. harlani* (Hall, 1843), *P. flabellus* (Miller and Dyer, 1878) and *P. wabanaensis* Fillion and Pickerill, 1990. Seilacher (1955) expanded the morphological limits of *Phycodes* and in doing so regarded *Arthropycus* Hall, 1852 as a junior synonym. Most subsequent authors, however, have distinguished these two ichnotaxa (e.g., Häntzschel, 1962, 1975; Osgood, 1970; Pickerill *et al.*, 1991). Herein we follow the suggestion of these latter authors. Thus *P. harlani* (Hall, 1843) should more appropriately be regarded as *A. harlani* Hall, 1852, considered by Häntzschel (1962, 1975) as the nomenclatural type. A more detailed discussion on the relationships of these ichnotaxa is given in Osgood (1970). *P. flabellus*, originally described by Miller and Dyer (1878) as *Lichrophycus flabellum*, is also characterized by distinctive transverse annulations and possibly could therefore also be regarded as an ichnospecies of *Arthropycus*. A re-examination of the type is clearly warranted, and for now we regard it as of uncertain status. *P. wabanaensis* was erected by Fillion and Pickerill (1990, p. 48) for "...*Phycodes*, in which a master tunnel branches at a very acute angle to form a broomlike burrow system. Proximal tube may be absent. Distal portion may also be composed of coalescent, nearly parallel, successive, retrusive, teichichnid burrows that are offset to the side..." This diagnosis corresponds closely to that of the ichnotaxon *Caugichnus* Hofmann, 1979, except that in the latter there is no master tunnel and instead it is characterized by multiple-entry systems. Additionally, *Caugichnus* possesses both protrusive and retrusive spreiten. We therefore regard *P. wabanaensis* and *Caugichnus* as distinctive and separate ichnotaxa.

Specimens from the Wapske Formation clearly represent a new ichnospecies of *Phycodes*. Individual burrow systems comprise 2 to 5 bundled sets that each branch horizontally in a

Fig. 5. Representative sketches of ichnospecies of *Phycodes* Richter, 1850. For those ichnospecies previously named in the literature but not figured here see text for details. (1) *P. coronatum* Crimes and Anderson, x 0.75 (to the left), x 1.55 (to the right) (after Crimes and Anderson, 1985, p. 329, figs. 11.1.3. Depository in Geological Survey of Canada, holotype GSC 73340). (2) *P.?* *antecedens* Webby, x 1.43 (after Webby, 1970, p. 102, fig. 20B. Depository in Palaeontological Collection of the Department of Geology and Geophysics, University of Sydney, paratype SUP 19895). (3) *P. pedum* Seilacher, x 0.72 (after Seilacher, 1955, pl. 25, fig. 3. Depository in Geologischen Instituts, Tübingen, holotype IC 1071/31). (4) *P. unguatus* Fillion and Pickerill, x 1.43 (after Fillion and Pickerill, 1990, p. 105, pl. 11, fig. 18. Depository in Geological Survey of Canada, holotype GSC 78188). (5) *P. curvipalmatum* Pollard, x 1.10 (after Pollard, 1981, p. 576, text-figs. 7a,b. Depository in special collections, Geology Department, University of Manchester, holotype MGSF32). (6) Holotype of *P. templus* Han and Pickerill, x 0.50 (NBMG 9202). (7) *P. auduni* Dam, x 0.97 (after Dam, 1990, p. 136, fig. 13C. Depository in Geological Museum, University of Copenhagen, holotype MGUH 19628). (8) *P. wabanaensis* Fillion and Pickerill, x 1.00 (after Fillion and Pickerill, 1990, p. 105, pl. 11, fig. 19. Depository in Geological Survey of Canada, holotype GSC 78198). (9) *P. circinatus* Richter, x 0.49 (after Seilacher, 1955, p. 385, fig. 3b). (10) *P. bromleyi* Dam, x 0.49 (after Dam, 1990, p. 139, fig. 15. Depository in Geological Museum, University of Copenhagen, holotype MGUH 19627). (11) *P. reniforme* Hofmann, x 0.67 (after Hofmann, 1979, p. 48, fig. 9. Depository in Geological Survey of Canada, holotype GSC 54213). (12) *P. palmatus* Hall, no scale (after Hall, 1852, pl. 6, fig. 1. Depository in New York State Collection without number).



broomlike or flabellate fashion, thereby collectively forming an interconnected or slightly overlapping inverted pagoda-shaped outline. Although in some specimens this inverted pagoda-shaped outline is not particularly obvious, such examples do exhibit several broomlike bundles arranged along the main stem. This characteristic is radically different from most other previously described ichnospecies of *Phycodes*, several of which, namely *P. auduni*, *P. bromleyi*, *P. circinatus*, *P. flabellus*, *P. palmatus*, *P. reniforme*, *P. ungulatus* and *P. wabanensis*, typically exhibit only one discrete set of bundled burrows emanating from the proximal tunnels (Fig. 5). The presence of interconnected bundled sets characteristic of *P. templus* clearly differentiates it from these latter ichnospecies.

Superficially, specimens from the Wapske Formation most closely resemble the interwoven burrow network of *P. curvipalmatum* (Pollard, 1981, pl. 89, figs. 1-2, text-fig. 7e), but exhibit the following differences: (1) individual burrows and burrow sets in *P. templus* are larger; (2) the entire burrow systems in *P. templus* are larger; (3) *P. templus* has regular, systematically branched sets which exhibit a broomlike or flabellate form, whereas in *P. curvipalmatum* the branches are dichotomous or palmate; (4) the tunnels of *P. templus* branch out at acute angles from a center and only rarely bifurcate, while in *P. curvipalmatum* the interbranch angle, while mostly acute, can be up to 90°, and the tunnels mostly bifurcate; and (5) the tunnels of *P. templus* are essentially straight and increase in width distally while the tunnels in *P. curvipalmatum* are curved and taper outward.

Finally, *P. templus* differs from *P. pedum* by possessing several tunnels within a single bundled set. *P. pedum* is characterized by single burrows periodically branching on one or both sides of the master tunnel, the branches never being arranged in discrete sets. In comparison to *P. antecedens*, *P. templus* also exhibits bundled sets, a feature not present in the former ichnotaxon; additionally *P. templus* is considerably larger. The remaining ichnospecies, *P. coronatum*, is characterized by a circular burrow outline with vertical (and themselves unbranched) offshoots from the outer margin of the circle (Crimes and Anderson, 1985); it clearly differs from *P. templus* as described herein.

The only possible additional occurrence of *P. templus* was reported from shallow marine Mississippian strata of western Montana (Rodriguez and Gutschick, 1970, p. 436, pl. 10, fig. c). This specimen was documented as a trail of unknown affinity, possibly *Phycodes*. Although the branching angles of its tunnels are more acute than those in material from the Wapske Formation, we tentatively regard the specimen as conspecific. Narbonne (1981, p. 210) considered Rodriguez and Gutschick's (1970) specimen as synonymous with *Uchirites* Macsotay, 1967. However, in his original description, Macsotay (1967) made no reference to branching within *Uchirites*; indeed, none of his figured specimens illustrates branching. We therefore believe that the aforementioned specimen as more akin to *Phycodes*, particularly *P. templus*, though only include it as a tentative synonym pending examination of the specimen.

As with the interpretation of most previously documented ichnospecies of *Phycodes* (see previous references), worm-like organisms or possibly even arthropods were presumably responsible for the burrow systems. In view of the absence of external ornament on the burrow walls of *P. templus*, worm-like organ-

isms are most favoured. Interestingly, the presence in *P. templus* of a distinct mudstone lining (*sensu* Keighley and Pickerill, 1994) and a structureless fill does not immediately invite comparison of it having been produced by a deposit feeder, the traditional interpretation of *Phycodes* (e.g., Seilacher, 1955; Marintsch and Finks, 1982). More typically, deposit-feeding burrows, commonly being actively filled, contain some form of internal structuring (e.g., menisci) or faecal material produced by biological processing by the causative organism. In contrast, passively filled, formerly open burrow structures typically contain a massive and unstructured internal fill and, depending upon the geotechnical properties of the substrate at the time of production, will normally be lined (Bromley, 1990). However, of particular relevance are present-day examples of deposit-feeding polychaetes that secrete abundant mucous and produce actively filled, lined burrows (Schäfer, 1972; Aller, 1983). We envisage *P. templus* to have been produced in a similar fashion, that is, as a lined structure produced by a vagile deposit feeder. Given such an interpretation, the absence of any obvious internal structures within *P. templus* is enigmatic. Notably, however, all the material is preserved in positive hyporelief with only the external walls of individual burrows being exposed; no horizontally truncated material, that would reveal the nature of the burrow interior, is present in the collections. Thus, although transverse and longitudinal vertical sectioning and etching of several specimens failed to reveal any internal fabrics, it may be that an internal structure is present but is too subtle to discern, requiring natural weathering processes of truncated material to demonstrate its presence or otherwise.

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