

AFFINITY OF *TUBIPHYTES*

by ROBERT RIDING and LI GUO

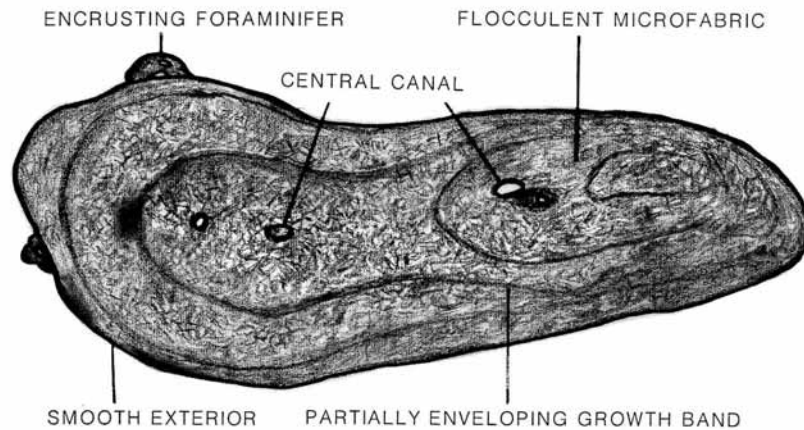
ABSTRACT. *Tubiphytes* Maslov, 1956 is a problematic fossil which ranges from early Carboniferous to mid-Cretaceous and is common in Permian and Triassic reef and other shallow marine carbonate facies. It has been suggested to be a cyanobacterium, hydrozoan, sponge, red alga, foraminifer, and a cyanobacterium-chlorophyte consortium. Its distinctive morphological features include densely flocculent and layered skeletal structure, an axial canal system which may or may not be integral to *Tubiphytes*, and smoothly rounded to encrusting external form. Cyanobacterial and algal affinities are discounted. A foraminiferal affinity cannot be ruled out, but is inconsistent with the morphology and organization of most *Tubiphytes*. The presence of an integral canal system would be consistent with a hydrozoan or sponge affinity, but the absence of other cavities in the skeleton which individuals could occupy does not favour a hydrozoan affinity. There is similarity between the skeletal structure of *Tubiphytes* and that of archaeocyath exothecal tissue and sponge filling tissue. *Tubiphytes* appears to have been capable of colonizing deeper and cooler water than algae with which it may also be associated. The family Nigriporellidae Rigby, containing *Tubiphytes*, is here regarded as belonging to the invertebrates, possibly the Porifera.

TUBIPHYTES is an important late Palaeozoic to Mesozoic reef-building organism which is widely regarded as an alga (Johnson 1963, p. 139; Croneis and Toomey 1965, p. 7; Flügel 1977, pp. 324–325; Flügel 1980, pp. 86–88; Flügel 1981a, p. 153; *Encyclopaedia Britannica* 1983, *Micropaedia X*, p. 167; Sartorio and Venturini 1988, p. 37). However, widely differing opinions concerning its affinity were expressed on the occasion of its discovery, which was made independently in the USSR and the USA during the 1950s. These questions concerning its affinity have not since been resolved. Although generally only a few millimetres in size, this fossil is a major contributor to Pennsylvanian, Permian and Triassic reefs and it is also often present in other shallow-marine carbonate facies. Its systematic position is therefore of ecological and sedimentary as well as evolutionary significance. Here we propose that a poriferan affinity accounts best for the canal system, banded structure, and flocculent skeletal fabric which are the most distinctive features of this genus.

DESCRIPTION

Tubiphytes is commonly irregularly cylindrical in form, or encrusting, with a smooth external surface and a distinctive dark, densely flocculent, internal structure which in detail appears to be composed of an irregular fibrous network. Internal tubes, which have been interpreted either as encrusted extraneous objects, or as a canal-system, are usually present. Spinose peripheral tubes have been reported in one instance (Flügel *et al.* 1984, pl. 31, fig. 6). The skeleton has a layered structure created by bands laid down successively around the central tube or tubes (Pl. 1). Variations in structure, style of encrustation, internal tubes, and inclusions are illustrated by Vachard (1980, fig. 67). *Tubiphytes* typically occurs as small (a few millimetres) individual masses, which may be irregularly branched, and also as thick (up to several centimetres) encrustations, usually on other skeletons such as sponges and bryozoans. Narrow tubiform fossils have also been compared with *Tubiphytes* (Flügel *et al.* 1984, pl. 42, fig. 9). The skeleton is generally very well preserved, sometimes in sharp contrast with associated skeletons (as noted by Rigby (1958, p. 584)) and its simple, smooth, dark appearance makes it conspicuous in thin-section.

Thus, the principal morphological features (Text-fig. 1) are: (a) the enclosed tube system; (b) the delicate, but generally well-preserved, flocculent network-like internal fabric; (c) the banded



TEXT-FIG. 1. Characteristic morphological features of *Tubiphytes obscurus* Maslov. Based on an Upper Permian specimen provided by David Edwards from the massive facies of the Capitan Reef Complex, Bat Cave Canyon, New Mexico, USA.

structure of the skeleton; and (d) the smooth, encrusting form with hemispherical to stolon-like protuberances.

HISTORY OF RESEARCH

Reviews of the progress of information and views concerning *Tubiphytes* have been made by Croneis and Toomey (1965), Flügel (1966, pp. 56–58), Ott (in Kraus and Ott, 1968), Flügel (1981a, 1981b), and Babcock (1977, pp. 17–18, 1986). For further information concerning taxonomy and distribution see also Vachard (1980, pp. 338–343) and Schäfer and Senowbari-Daryan (1983, pp. 126–129). The principal details are as follows.

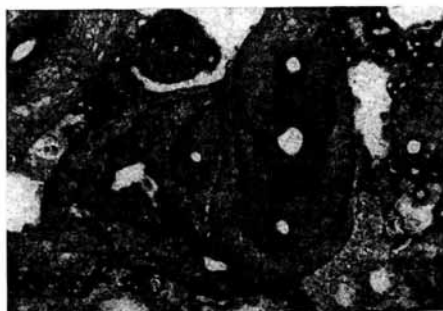
Maslov (1956, pp. 82–84) placed *Tubiphytes* in *algae incertae sedis* with the tentative suggestion that it could be a cyanobacterium (Schizophyta). Previously, Rauser-Chernousova (1951, p. 17 and pl. 3, figs 1–2) had named this fossil *Shamovella*, from the Kungurian (uppermost Early Permian) reefal sequences of the Sterlitamak–Ishimbay area, 125–150 km south of Ufa in the Bashkir Republic, just west of the southern Urals, providing illustration but not naming a type species (see Maslov 1956, p. 21; Elias 1959, p. 77). Elias (1959, p. 77) regarded *Shamovella* as a *nomen imperfectum* (see also Croneis and Toomey 1965, p. 7). In establishing *Tubiphytes*, Maslov used material from the same Sterlitamak–Ishimbay area that he and Rauser-Chernousova collected. It is clear from the illustration of *Shamovella* by Rauser-Chernousova (1951) reproduced by Elias (1959, pl. 1, fig. 6) that it is the same as *Tubiphytes* Maslov. Meanwhile, in the United States, in rocks of only slightly younger age (the Capitan reef complex of New Mexico and Texas (Newell *et*

EXPLANATION OF PLATE I

Figs 1–4. *Tubiphytes obscurus* Maslov. Upper Permian, massive facies of the Capitan Reef Complex; Bat Cave Canyon, New Mexico, USA; thin-section photomicrographs showing characteristic features of the type-species (see also Text-fig. 1): smooth exterior, dense, dark flocculent internal microfabric, enveloping to partly enveloping growth bands, and central tubular structures. All specimens courtesy of David Edwards. 1, $\times 32$. 2, $\times 18$. 3, $\times 18$. 4, $\times 35$. Note in figure 4 that the central tube resembles a nubeculariid foraminifer (cf. Flügel 1981b, figs 4–5; and Bernier 1984, pl. 21, figs 1–2), although if the short side branches are regarded as tubes then they also resemble sponge oscula (Colin Scrutton, pers. comm. 1990).



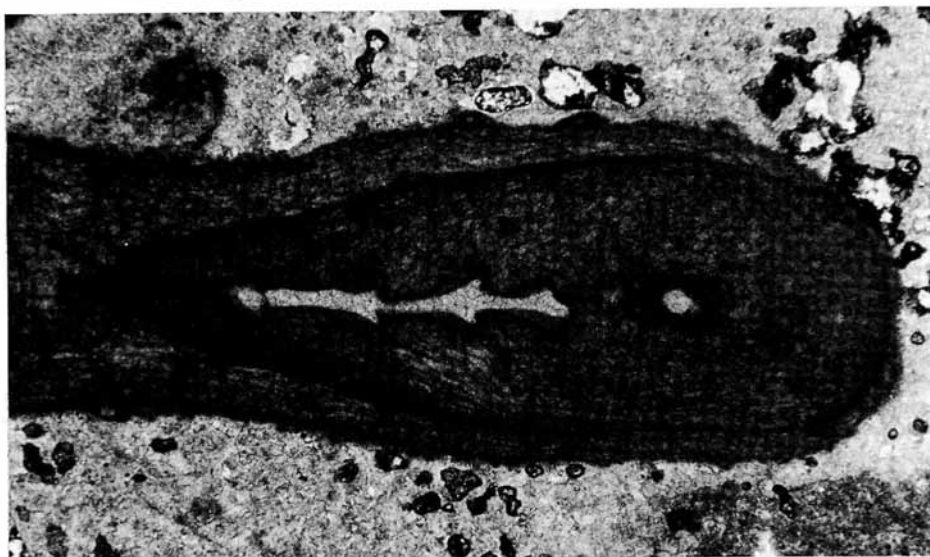
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al. 1953, p. 112, pl. 17, fig. 3; pl. 18, figs 1–2, 5–6) and in the Chinati and Glass Mountains of Texas (Newell 1955, p. 307, pls 4–8)), this fossil had been noticed as a frame-building organism. It was not named, but was regarded as a hydrocoralline (= hydrozoan) following advice from J. H. Johnson: 'a problematical encrusting and stoloniferous organism, considered by J. H. Johnson (personal communication) as possibly a hydrocoralline' (Newell *et al.* 1953, p. 112). Newell *et al.* (1953, p. 112) distinguished it from *Solenopora* (see discussion of rhodophyte affinity, below) and Newell (1955, p. 307, pl. 8) noted its 'indistinct internal network suggestive of communicating canals or spicules'.

Shortly after this, Rigby (1958), using material mainly from the middle Permian of Texas, described the same fossil as a new genus, *Nigriporella*, which he placed in a new hydrozoan family, the Nigriporellidae. Konishi (1959) recognized that *Nigriporella* was a synonym of *Tubiphytes*, and also favoured a hydrozoan affinity for it. He noted that it is widespread in the Permian and figured an example from the Lower Permian of Honshu, Japan. Hudson (1960) and Elliott (1962) recorded *Tubiphytes* in the Permian of Oman and northern Iraq respectively, but did not add to views about its affinities.

Although instrumental in first suggesting a hydrozoan affinity to American workers, ten years later Johnson (1963, p. 139) followed Maslov in placing *Tubiphytes* in 'algae of uncertain systematic position', as did Croneis and Toomey (1965). Flügel (1966, p. 56) regarded *Tubiphytes* as a microproblematicum, but in a discussion of affinities mentioned the possibility of a comparison with rhodophytes. This was the first departure from the 'algal' affinities proposed by earlier authors which had actually implied blue-green rather than eukaryote algae.

From this point onwards three strands of opinion can be followed through to the present: sponge/animal, rhodophyte alga, and cyanobacterium or cyanobacterial-chlorophyte consortium. Ott (*in* Kraus and Ott 1968, p. 271) suggested that *Tubiphytes* may be a sponge. Crescenti (1969), describing a new species, *T. morronensis*, from the uppermost Jurassic of the central Apennines in Italy, preferred Maslov's view that it is an *alga incertae sedis*. Homann (1972) and Kochansky-Devidé (1970) supported Flügel's (1966) suggestion of a rhodophyte affinity, although it should be noted that here Kochansky-Devidé was referring not to *Tubiphytes obscurus* Maslov but to *T. carinthiacus* (Flügel), a species originally placed by Flügel (1966, p. 54) in *Hikorocodium* Endo.

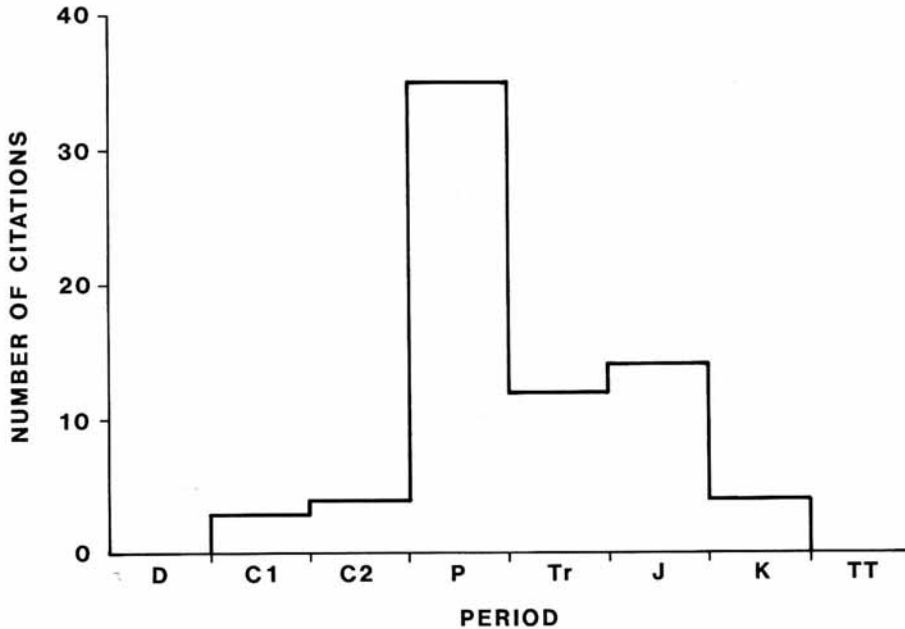
Toomey (1969, pp. 1323–1324) reiterated the possibility of a cyanobacterial origin, and Flügel (1979, p. 578) and Flügel and Flügel-Kahler (1980, pp. 164, 172) also tentatively returned to this opinion. Babcock (1977, pp. 17–18) briefly reviewed the affinities which had been proposed and concluded that neither a hydrozoan nor a cyanobacterial affinity for *Tubiphytes* seemed likely, although later (Babcock 1979, p. 425) he expressed the view that *Tubiphytes* is an animal rather than an alga or cyanobacterium. Flügel (1981a), referring to *T. carinthiacus*, cast doubt on Babcock's (1977, p. 18) criticism of the blue-green algal hypothesis, and echoed Maslov: 'These arguments are not valid if we consider the interwoven threads seen in *Tubiphytes carinthiacus* as remains of trichomes', adding 'The spar-filled "tubes" may belong to another alga, which could have been circumscribed by *Tubiphytes*. Associations of epiphytes consisting of filamentous blue-green algae and filamentous green algae are known from modern environments' (Flügel 1981a, p. 153). Flügel (1983) restated this view that a cyanobacterial-chlorophyte and algal-foraminiferal consortium could be responsible for *Tubiphytes*.

Babcock (1986, pp. 15–17) again reviewed the genus in some detail, emphasizing its problematic nature. In a general systematic treatment of calcified cyanobacteria and algae, Luchinina (*in* Chuvashov, Luchinina and Shuysky *et al.* 1987, p. 30) placed *Tubiphytes* together with fossils such as *Girvanella* Nicholson and Etheridge. A genus somewhat similar to *Tubiphytes*, *Plexoramea* Mello from the Triassic, which had at times been referred to as *Tubiphytes carinthiacus* (which itself was originally described as *Hikorocodium carinthiacum* Flügel: see Systematic Palaeontology, below) has been compared with both chlorophyte algae and fungi (Flügel *et al.* 1988). *Plexoramea* has a more open internal mesh-like fabric than *Tubiphytes obscurus*. We have drawn attention to the similarity between the microfabric of *Tubiphytes* and that of some archaeocyath tissue (Guo and Riding 1989). The latter is dense, dark, flocculent and also shows banding reminiscent of that seen

in *Tubiphytes*. However, we have not observed a delicately fibrous fabric quite like that of *Tubiphytes*, nor are similar axial canal-systems present and the similarity, although intriguing, remains superficial.

DISTRIBUTION

Tubiphytes ranges from Early Carboniferous to mid-Cretaceous (Text-fig. 2). It first occurs in the Mississippian of Utah, USA (Rigby 1958, p. 586). The youngest record appears to be that of *T. morronensis* by Crescenti (1969, p. 37) from the early Albian (mid-Cretaceous) of central Italy. *Tubiphytes* becomes conspicuous in the Pennsylvanian, where it is best known in the south-western United States (Toomey 1969), and common in the Early Permian (Malek-Aslani 1970; Wahlman 1985, 1988). Newell *et al.* (1953, p. 112) noted the abundance of what later would be recognized as *Tubiphytes* in the Capitan reef complex (see also Achauer 1969; Kendall 1969; Babcock 1977, 1979) and the genus is widely distributed in Permian reefs of the Mediterranean area and elsewhere (Flügel 1984, fig. 4), often in association with another problematical genus, *Archaeolithoporella* Endo (Flügel 1981a). *Tubiphytes* is also important in Middle Triassic reefs (Ott 1967; Brandner and Resch 1981, p. 212), and in the Upper Triassic (Flügel 1981c; Schäfer and Senowbari-Daryan 1983). Jurassic reports include *Tubiphytes* from the middle–upper Oxfordian of Franconia, West Germany (Flügel and Steiger 1981, p. 378), Kimmeridgian of the French Jura (Bernier 1984, p. 524), middle Kimmeridgian and lowermost Tithonian of Franconia (Flügel 1981b), and the middle to upper Jurassic of central Italy (Crescenti 1969, p. 21; Chiocchini *et al.* 1980). Barattolo and Pugliese (1987, pls 32, 40) figure *Tubiphytes* from the middle–upper Jurassic (Callovian–Oxfordian) and Jurassic–Cretaceous (Portlandian–Berriasian) of Capri, Italy. Jansa *et al.* (1982) report *Tubiphytes* from Berriasian–Valangian (early Cretaceous) sponge bioherms of the Scotian Shelf of off-shore



TEXT-FIG. 2. Histogram of published references to *Tubiphytes* by geological period. Data from GEOREF database 1989 and references cited in text.

eastern Canada. Misik (1979, p. 709) reports *T. obscurus* from the Triassic to Neocomian of the western Carpathians without indicating the precise age of the Lower Cretaceous occurrences. Crescenti (1969, pp. 21–22, 37) also recorded *Tubiphytes* from the Lower Cretaceous (up to early Albian) of central Italy.

Although *Tubiphytes* is important in shallow-water limestones, it also occurs in the deeper parts of Permian reefs at Trogkofel in the Carnic Alps (David Edwards, pers. comm. 1989) and at Capitan (Babcock 1977, fig. 16; 1979, fig. 3). At Capitan it also occurs in cryptic reef habitats (J. A. Babcock, pers. comm. 1990). Sponge bioherms containing *Tubiphytes* from the early Cretaceous of the Scotian Shelf are interpreted to have formed at a depth of 60–100 m (Jansa *et al.* 1982). Furthermore, *Tubiphytes* is common in Lower Permian limestones of West Timor (Indonesia), where it is associated with a temperate climate brachiopod fauna (Riding and Barkham in prep.). In this West Timor occurrence, dasycladaleans, gymnocodiaceans, and other algae of warm-water environments are absent and *Tubiphytes* occurs with bryozoans, crinoids and brachiopods. These indications that *Tubiphytes* could inhabit a temperate water environment (West Timor) and also relatively deep (Trogkofel, Capitan, Scotian shelf), and cryptic (Capitan), reefal environments strengthen the view that it is unlikely to be a cyanobacterium (or a green alga).

DISCUSSION

Affinities which have been suggested for *Tubiphytes* include cyanobacterium, hydrozoan, sponge, rhodophyte, foraminifer and cyanobacterium–chlorophyte consortium (Table 1). The distinctive morphological features of the genus include dense flocculent fabric, central tube (canal system?), layered structure, and smooth, simple, external form (Text-fig. 1).

Cyanobacterium

Maslov (1956, pp. 82–84; for English translation see Croneis and Toomey 1965, p. 8) regarded the tube of *Tubiphytes obscurus* as a trace of a stem, or some such extraneous object, which *Tubiphytes*

TABLE 1. Summary of the affinities which have been suggested for *Tubiphytes*, showing the originator (first author), basis for the original interpretation, problems or supporting evidence, and ranking of the affinities in order of likelihood.

Proposed affinity	First author	Original reasons	Problems or support	Likelihood
Poriferan	Ott (In Kraus and Ott 1968)	?	Microfabric resembles sponge filling tissue; growth style (shape, banding) is generally poriferan	1
Foraminifer	Bernier 1984	Morphology of tubular forms	May apply to <i>T. gracilis</i> and <i>T. morronensis</i> but morphology and structure of <i>T. obscurus</i> is inconsistent with a foraminiferal affinity	2 (but does not apply to type-species)
Hydrozoan	Rigby 1958	Canal system	'Canal' may not be integral parts of the skeleton; no zooid receptacle evident	3
Cyanobacterium	Maslov 1956	Microfabric	No close resemblance to known calcified cyanobacterial microfabrics	4
Cyanobacterial chlorophyte consortium	Flügel 1981	?		4
Rhodophyte	Flügel 1966	?	No close resemblance to known calcified rhodophytes	5

encrusted. He therefore concentrated on the delicate irregular meshwork-like structure of the skeleton, which he compared with the trichomes of cyanobacteria. This view has been supported by Flügel (1981a, p. 153), particularly with respect to *T. carinthiacus*. Nevertheless, it would seem that the tubes of *Tubiphytes* cannot so readily be disregarded (see discussion of hydrozoan affinity, below). However, the main objections to a cyanobacterial affinity for *Tubiphytes* are that masses of unorientated trichomes are not known to assemble in this fashion, and that it is not the trichomes (the strands of cells) but the enveloping mucilaginous sheath that is the site of calcification in cyanobacteria (Pentecost and Riding 1986, p. 76). This results in solid or tubiform fossils which are comparable with modern calcified cyanobacteria (Riding 1991a), but which do not resemble the delicate anastomosing network seen in *Tubiphytes*. Maslov (1956, p. 83) was incorrect when he compared this supposed style of fossilization 'for calcareous blue-green algae with very thin trichomes' with that of *Epiphyton* Bornemann, which is common in the Cambrian. In fact, *Epiphyton* has a dense micritic microfabric in which reports of cells have not been confirmed (Riding 1991b). Furthermore, *Tubiphytes* does not exhibit the fabrics, or contain the extraneous particulate material, typical of cyanobacterial oncoids.

Hydrozoan

Tubiphytes is an encrusting organism, and clearly was capable of overgrowing and surrounding adjacent objects. However, it also contains tubes which do appear to be, as even Maslov's name for the genus implies, an integral feature, commonly occupying an axial position in the skeleton. This construction has no analogue among the cyanobacteria or algae. Rigby (1958) was the first to emphasize the tubes. His interpretation of them as representing a canal-system resembling that of hydrozoans, stromatoporoids and sponges is in marked contrast to Maslov's interpretation. Presumably, similar considerations influenced J. H. Johnson's advice to Newell *et al.* (1953, p. 112) suggesting a hydrocoralline (i.e. hydrozoan) affinity for what would subsequently be recognized as *Tubiphytes* in the Capitan reef complex, but this was only a brief personal communication. Rigby's (1958) description of *Nigriporella* is detailed. He regarded the tubes as an integral part of the skeleton, and he discerned similarities with both milleporids and stromatoporoids. He emphasized the 'zooidal tubes connected by a small meandering canal system', identified dactylopores and gastropores (Rigby, 1958, pp. 583–584, text-fig. 2), and particularly compared them with the tubes and canals of milleporids. However, he compared the layered structure of *Nigriporella* with stromatoporoid latilaminae (subsequently, stromatoporoids have come to be widely regarded as sponges, see Poriferan affinity, below). In discussing relationships, Rigby noted that 'Superficially, zooidal tubes of *Nigriporella* resemble canals of sponges', but continued 'chambered tubules and lack of definite skeletal elements akin to spicules make it impossible to class the genus with sponges' (but see Poriferan affinity, below). He concluded, 'Nigriporellids are considered as hydrozoans because of their mode of growth, presence of two types of zooidal tubes, and latilamellar structure' (Rigby 1958, p. 584).

Nevertheless, uncertainties still exist. The tube system of *Tubiphytes* does not generally appear to be so organized as Rigby (1958) described it. The central tube does, in fact, in some cases appear to be an encrusted object, as Maslov (1956) observed (see Foraminifer, below). Also, Rigby's (1958) discussion of hydrozoan versus sponge features needs to be reassessed in the light of subsequent work on fossil sponges. The main feature apparently lacking in *Tubiphytes*, which makes a hydrozoan affinity particularly difficult to support, is a receptacle in which individual zooids could have been housed.

Rhodophyte

Croneis and Toomey (1965), in summarizing the work of the previous fifteen years, contrasted the Johnson/Newell/Rigby hydrozoan view, which was supported by Konishi (1959), with the Maslov/Rausser-Chernousova 'algal' view because it was commonplace at that time to regard blue-greens as algae. However, the idea of an algal affinity in the strict sense, meaning a eukaryote as opposed to a blue-green alga or cyanobacterium, was not actually mentioned until Flügel (1966, p. 58)

tentatively suggested that a rhodophyte affinity might be considered. This was re-stated by Homann (1972, p. 256) for *T. obscurus* and, with respect to *T. carinthiacus*, by Kochansky-Devidé (1970), but has not since been supported. In fact, Newell *et al.* (1953, p. 112) had already compared *Tubiphytes* with *Solenopora*: 'Superficially it has somewhat the general expression of the coralline alga *Solenopora*, forming lamellar expansions, rounded tubercles, and ramose cylindrical branches. Internally the fossil is nearly structureless except for apparently erratic tubular pores or perforations. It is distinguished in thin sections from *Solenopora* by finer and less regular structure and by opacity ...'. The central tube of *Tubiphytes* does not resemble rhodophyte conceptacles (cf. Flügel 1966 and Homann 1972) and the closest comparison that could be drawn with extant calcified red algae would be with the perithallic tissue of crustose corallines, but this has a gridlike appearance which, as Newell *et al.* (1953) noted, is more orderly than that of *Tubiphytes*, and this affinity could not account for the tubes.

Poriferan

Since Rigby's (1958) study of *Tubiphytes*, several fossil groups, including Palaeozoic stromatoporoids (see Stearn 1975; Wood 1987), chaetetids (Gray 1980), and many Mesozoic genera previously attributed to the hydrozoans and tabulozoans (Flügel 1981*b*), have come to be regarded as likely to be sponges. This re-evaluation is both due to discovery of modern analogues, particularly sclerosponges, and to more critical comparative assessment of affinity.

Ott (in Kraus and Ott 1968, pp. 269–273) in a review of the systematics of *Tubiphytes* suggested that it could be a sponge and stated his intention to publish details of this novel suggestion separately. However, this publication did not take place. Several features suggest that *Tubiphytes* could be a sponge. Rigby's (1958, p. 584) rejection of a sponge affinity for *Tubiphytes* on the basis of absence of spicules and presence of chambered tubules is not now valid, but similarities which he noted remain significant. The tubes of *Tubiphytes* do, as Rigby (1958, p. 584) stated, 'resemble canals of sponges'. The banding, which Rigby (1958, p. 583) compared with stromatoporoid latilaminae, also resembles the growth style of sponges (for example, see the enveloping layers of the Wolfcampian calcisponges figured by Wahlman 1988, fig. 9*c*). The flocculent fabric of the skeleton resembles that of exothecal tissue of archaeocyaths (Guo and Riding 1989). It is suggested here that it may be comparable with the vesicular filling tissue of calcisponges (see Hartman *et al.* 1980, p. 208). Furthermore, the smooth encrusting and protuberant external form of *Tubiphytes* is typical of some sponges. However, the apparent absence of external pores is an obstacle to this interpretation.

Cyanobacterial–chlorophyte consortium

Flügel (1981*a*, 1983) suggested that *Tubiphytes* might be a cyanobacterial–chlorophyte consortium, but this interpretation has not been further developed and does not appear to have support from modern analogues.

Foraminifer

Bernier (1984, pp. 523–524) regards *T. morronensis* as a nubeculariid foraminifer. However, this view may be encouraged by the ability of *Tubiphytes* to encrust foraminifers which then become incorporated as a central tube. The Bajocian–Kimmeridgian specimens of *T. morronensis* figured by Crescenti (1969, figs 20–22) show a central tube with constrictions. Bernier's (1984, pl. 21, figs 1–2) illustrations even more clearly show a linear sequence of flask-like swellings which in size and appearance closely resemble uniserial chamber arrangement in foraminifers. This has also been noted by Vachard (1980, p. 340 and fig. 67 (2)). The miliolacean nubeculariid foraminifer *Nodophthalmidium* Macfadyen has been reported forming the nucleus of encrusting *T. morronensis* from the Upper Jurassic of Franconia, southern Germany (Flügel 1981*b*, p. 136, figs 4–5). Similar morphologies are shown by the 'axial canal-like' structures of specimens from the Upper Permian Capitan Reef Complex (Pl. 1, fig. 4) and from the mid-Permian of eastern Afghanistan (Vachard and Montenat 1981, pl. 2, fig. 3). However, whereas Flügel (1981*b*) interprets *T. morronensis* to be

encrusting a foraminiferal nucleus, Bernier (1984, p. 523) takes the view that the fine tissue of *Tubiphytes* itself is comparable with the wall-structure of miliolid foraminifers, and he compares the whole fossil, both central tube and surrounding dense skeleton, with the nubeculariid genus *Cornuspiramia* Cushman.

The generally much greater thickness of the wall in *Tubiphytes obscurus*, its banded structure and distinctive flocculent, rather than densely micritic, fabric, would appear to preclude the possibility of a foraminiferal affinity. Tubiform fossils with wall-structure resembling that of *Tubiphytes* have been described from the Permian, and it has been suggested that they may be small specimens of *T. gracilis* Schäfer & Senowbari-Daryan (Flügel *et al.* 1984, p. 208, pl. 42, fig. 9). It is therefore possible that some specimens referred to *Tubiphytes* may be foraminifers and this requires clarification. However, there seems little likelihood that *Tubiphytes* itself can be attributed to the foraminifers. The interpretation of Flügel (1981*b*) that nubeculariid foraminifers can act as substrates for encrustation by *Tubiphytes* is accepted here. It is also worth noting that the apparent short side tubes of the axial tube (see Pl. 1, fig. 4) resemble sponge oscula, although if they are actually continuous flanges then they better resemble foraminifer chambers.

Synthesis

Tubiphytes does not appear closely to resemble any extant organism and no convincing parallels can be drawn between it and calcified cyanobacteria or algae. There have been few comparisons made between *Tubiphytes* and other fossils. Examples include the Triassic genus *Plexoramea* (which probably should be classified in the same group as *Tubiphytes*), Rigby's (1958) comparison of *Tubiphytes* with stromatoporoids (a similarity which he did not regard as close), and Maslov's (1956) mention (discounted here) of *Epiphyton*. The significance of the similarity between the skeletal fabric of *Tubiphytes obscurus* and the exothecal tissue of some archaeocyaths (Guo and Riding 1989) is still uncertain.

The canal system, in particular, is crucial to discussion of *Tubiphytes*. If it is integral to the fossil, then it links this genus most closely with animals such as hydrozoans and sponges. An invertebrate affinity is consistent with the ability of *Tubiphytes* to live in relatively cooler (Riding and Barkham, in prep.) and deeper water environments than algae such as dasycladaleans, phylloids, gymnocodiaceans and solenoporaceans, with which it co-exists in shallow warm water environments. In the choice between a hydrozoan or a sponge, the absence of receptacles to house individuals (see Stearn 1982, p. 513) favours a poriferan affinity.

CONCLUSIONS

The widely quoted cyanobacterial affinity for *Tubiphytes*, proposed by Maslov (1956, p. 82) is based on comparison of the flocculent skeletal structure with trichomes. However, this flocculent structure does not have any parallels in known calcified cyanobacteria and algae. There is at present no good evidence to suggest that *Tubiphytes* is a cyanobacterium, alga, or consortium of cyanobacteria and algae. Maslov (1956) believed that the tubes, for which he named the genus, were extraneous objects. It is clear that foraminiferal tubes, for example, can be enveloped by *Tubiphytes*. However, the possibility, documented in detail by Rigby (1958), cannot be ruled out that the tubes represent a canal system which is present as an integral part of the fossil and not as remains of objects which *Tubiphytes* encrusted. The presence of a canal system indicates an invertebrate affinity, particularly hydrozoan or poriferan.

There has been considerable confusion between hydrozoans and sponges in both the Palaeozoic and the Mesozoic. The absence of sites within or upon the skeleton which could have housed individuals is a factor which does not support a hydrozoan affinity. On the other hand, the presence of tabulae across tubes, and also the absence of spicules, which led Rigby (1958, p. 584) to reject a sponge affinity, would not now be regarded as excluding this possibility. The canal system does, as Rigby (1958, p. 584) pointed out, resemble that of sponges, and the other internal and external features of *Tubiphytes* are consistent with a sponge affinity.

Tubiphytes is present not only in the upper parts of reefs and in other shallow-water environments, but also in the deeper parts of reefs such as Capitan (Babcock 1977, 1979) and Trogkofel (David Edwards pers. comm. 1989). There is also evidence in the Permian that it was capable of inhabiting temperate water environments where dasycladaleans, gymnocodiaceans and calcified cyanobacteria were absent (Riding and Barkham in prep.). These environmental tolerances are consistent with an invertebrate affinity.

Tubiphytes obscurus Maslov, the type-species, has a distinctive dense dark skeletal structure. This wall appears to be too thick to be comparable with that of foraminifers (but cf. Bernier 1984, and Flügel *et al.* 1984, pl. 42, 9) and there seem to be no other parallels among late Palaeozoic and early Mesozoic fossils. However, it is similar to the exothecal tissue of Lower Cambrian archaeocyaths, whose systematic position is also problematic but for which a poriferan affinity is now considered likely (see Debrenne and Vacelet 1984).

Therefore, the available evidence does not support a cyanobacterial or algal origin for *Tubiphytes*. Its environmental distribution is consistent with an invertebrate affinity and its general skeletal structure and organization suggest that it is a hydrozoan or sponge, although a foraminiferal affinity cannot be ruled out. On balance, morphological evidence at present indicates that a poriferan affinity is the most likely one for *Tubiphytes*.

SYSTEMATIC PALAEOLOGY

INVERTEBRATA

Phylum ?PORIFERA

Family NIGRIPORELLIDAE Rigby, 1958

Although *Nigriporella* is a junior synonym (of *Tubiphytes*) this does not invalidate the family name (for taxonomic description see Rigby (1958, p. 583)).

Genus TUBIPHYTES Maslov, 1956

- 1951 *Shamovella* Rauser-Chernousova invalid genus
 1956 *Tubiphytes* Maslov, p. 82
 1958 *Nigriporella* Rigby, p. 584

Description. For taxonomic description see Maslov (1956, p. 82). Konishi (1959) recognized that *Nigriporella* is a synonym of *Tubiphytes* although he did not specifically state that it is a junior synonym. Johnson (1963, p. 139) considered that *Tubiphytes* 'closely resembles Johnson's and Konishi's *Retaphycus* from the Mississippian of Alberta (Johnson and Konishi, 1956, p. 103, pl. 7). It appears to differ only in having a coarser texture and a somewhat different growth form.' However, these illustrations of *Retaphycus* show neither the central canal-system nor the layered structure which are typical of *Tubiphytes* and we conclude that they are not related. *Plexoramea* (Mello 1977, pp. 190–192) is, however, similar to *Tubiphytes* (for details see Flügel *et al.* 1988).

Discussion. Seven species referable to *Tubiphytes* have been described:

- T. obscurus* Maslov, 1956, p. 82, pl. 25, figs 1, 3; pl. 26, pl. 27, figs 1–3; the type-species.
N. magna Rigby, 1958, p. 584, pl. 86, fig. 1.
N. minima Rigby, 1958, p. 585, pl. 86, figs 2–3.
T. carinthiacus (Flügel 1966) Kochansky-Devidé 1970, p. 244, pl. 20, figs 1–2 (= *Hikorocodium carinthiacum* Flügel 1966, p. 54, pl. 10, figs 1–5).
T. morronensis Crescenti, 1969, p. 35, figs 10, 20–22.
T. gracilis Schäfer and Senowbari-Daryan, 1983, p. 128, pl. 10, figs 1, 8.
T. multisiphonatus Schäfer and Senowbari-Daryan, 1983, p. 129, pl. 10, figs 5–7.

Plexoramea cerebriformis has on a number of occasions been confused with *T. carinthiacus* (see Flügel *et al.* 1988). Misik (1979, p. 709) regards *T. morronensis* as a junior synonym of *T. obscurus*.

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