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Enigmatic tubes associated with microbial crusts from the Late Jurassic of the Northern Calcareous Alps (Austria): a mutualistic sponge–epibiont consortium?

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Irregular tube-shaped microfossils incertae sedis are a typical constituent of Late Jurassic shallow-water reefal carbonates of the Northern Calcareous Alps of Austria and are described in open nomenclature. The enigmatic, polymorphous spar-filled tubes with neither observable external nor internal skeletal elements occur either free within peloidal sediments or mostly fixed to skeletal substrates embedded in microbial crusts including the genera *Labes* Eliášová, *Crescentiella* Senowbari-Daryan *et al.* or *Isnella* Senowbari-Daryan. The tubes are varied in shape and closely resemble different taxa of sponges. As the microbial crusts preferentially occur associated with these tubiform microfossils, this association is suggested to be non-parasitic and mutualistic. Without the surrounding crusts, the existence of these animals would have been masked or perhaps even totally lost in the fossil record expressing the importance of these findings as a characteristic element in the inventory of Late Jurassic reefal biocoenoses. ☐ *Eastern Alps, Late Jurassic, microbial crusts, mutualism, sponges, Tethys Ocean.*

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Late Jurassic shallow-water carbonates in the Northern Calcareous Alps (NCA) (Fig. 1A, B) of Austria known as Plassen Formation of the Plassen Carbonate Platform are reported from various today isolated occurrences. These occurrences belong to different palaeogeographically independent and isolated carbonate platforms of the Plassen Carbonate Platform system, each prograding towards deep-water radiolarite basins (Figs 1C and 2). These have been investigated recently with respect to facies, micropalaeontology and biostratigraphy (e.g. Schlagintweit *et al.* 2003, 2005; Gawlick *et al.* 2004). The majority of these localities are concentrated in the central NCA, mainly the Salzkammergut area with the type-locality Mount Plassen (Fig. 1B). The latter exposes the complete sedimentary sequence comprising an initial Kimmeridgian shallowing-upward succession, lagoonal limestones of latest Kimmeridgian-Tithonian age, ?Early Berriasian backreef to slope sediments representing a deepening upward, and final drowning in the Berriasian (Gawlick & Schlagintweit 2006). There are two intervals of coral-stromatoporoid reefal limestones, the first in the Late Kimmeridgian and a second in the Late Tithonian (?pro parte Early Berriasian) (Fig. 1A). These fossiliferous limestones contain calcareous algae (mainly Dasycladales), benthic foraminifera and a considerable number of predominantly encrusting microorganisms of unknown systematic position (microproblematica). The frontal parts facing the platform slopes are characterized by boundstones containing a diverse association of microencrusters (e.g. *Crescentiella morronensis*, *Iberopora bodeuri*, *Koskinobullina socialis*, *Radiomura cautica*), and variable amounts of syngenetic cement crusts (Schlagintweit & Gawlick 2008). Tube-shaped microproblematica often associated with crusts of assumed microbial origin occur especially in these boundstones. In the present paper these microproblematica are described and their systematic position and mutual relationships with the surrounding crusts are discussed. The specimens are described from thin sections derived (in alphabetical order) from Mount Drei Brüder, Mount Jainzen, Mount Krahstein, Mount Lugberg, Mount Rettenstein and Mount Trisselwand (Fig. 1B).

Tube morphotypes

Due to their peculiar shapes, pointing to a biogenic origin, these are here referred here to as tubes and not as cavities. They occur either free within fine-grained peloidal packstones or fixed to hard substrates (Fig. 3); especially in the latter they display encrustations with *incertae sedis* of supposed microbial affinities. In all tubes the central hollow is composed of sparry

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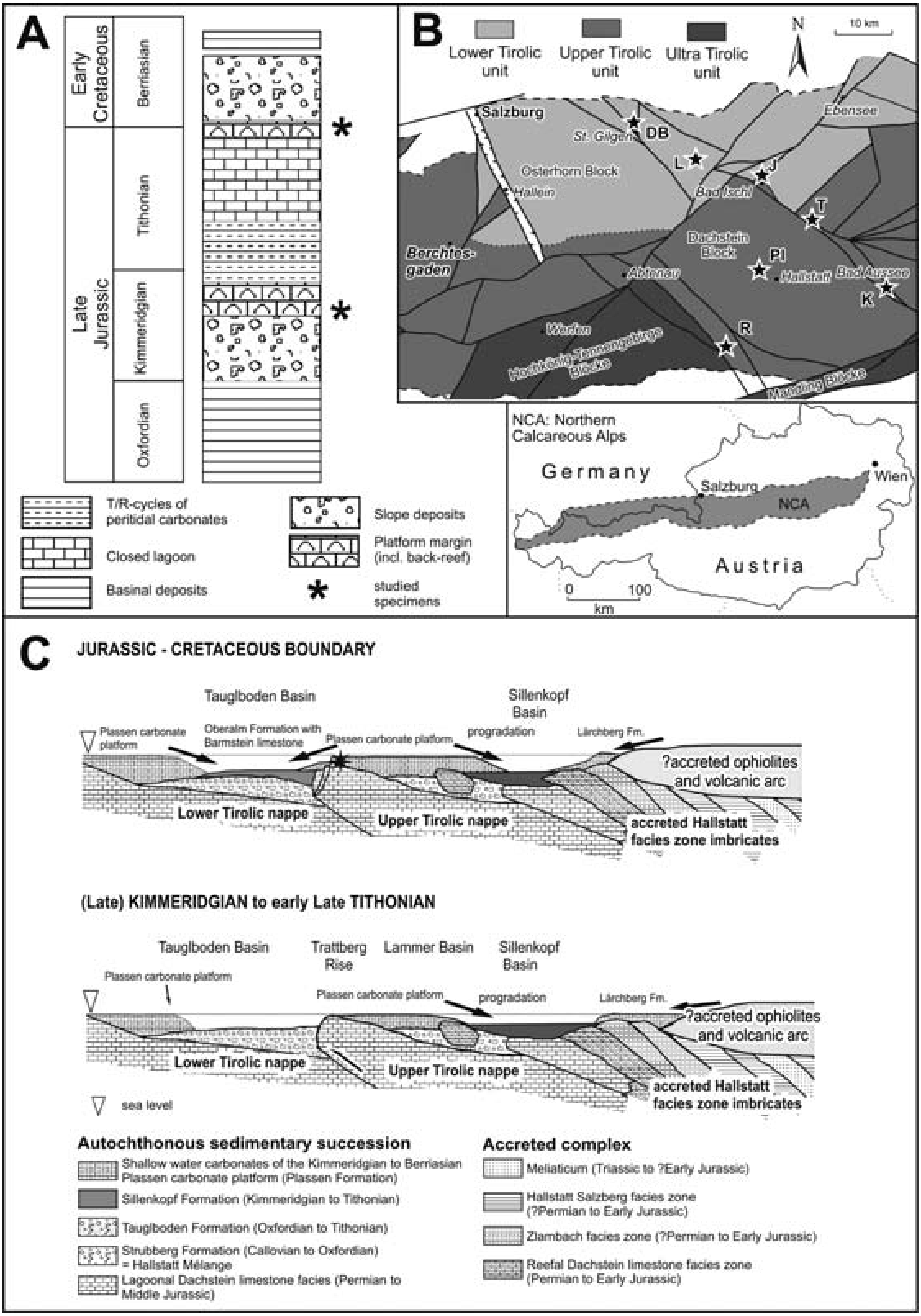

Fig. 1. A. Schematic profile of the Plassen Carbonate Platform at Mount Plassen (based on Schlagintweit *et al.* 2003, 2005) with indication of the two reefal intervals from which the studied material were derived. B. Block tectonic framework of the middle part of the Northern Calcareous Alps (from Frisch & Gawlick 2003); asterisks mark the sample localities (DB = Drei Brüder, J = Jainzen, K = Krahstein, L = Lugberg, R = Rethenstein, T = Trisselwand) and the type-locality of the Plassen Formation Mount Plassen (PL). C. Framework of Late Jurassic to Early Cretaceous platform-basin reconstruction (after Gawlick & Schlagintweit 2006). Late Kimmeridgian and Late Tithonian are the times of maximum platform growth with rapid progradation towards and over the radiolaritic basins in between.

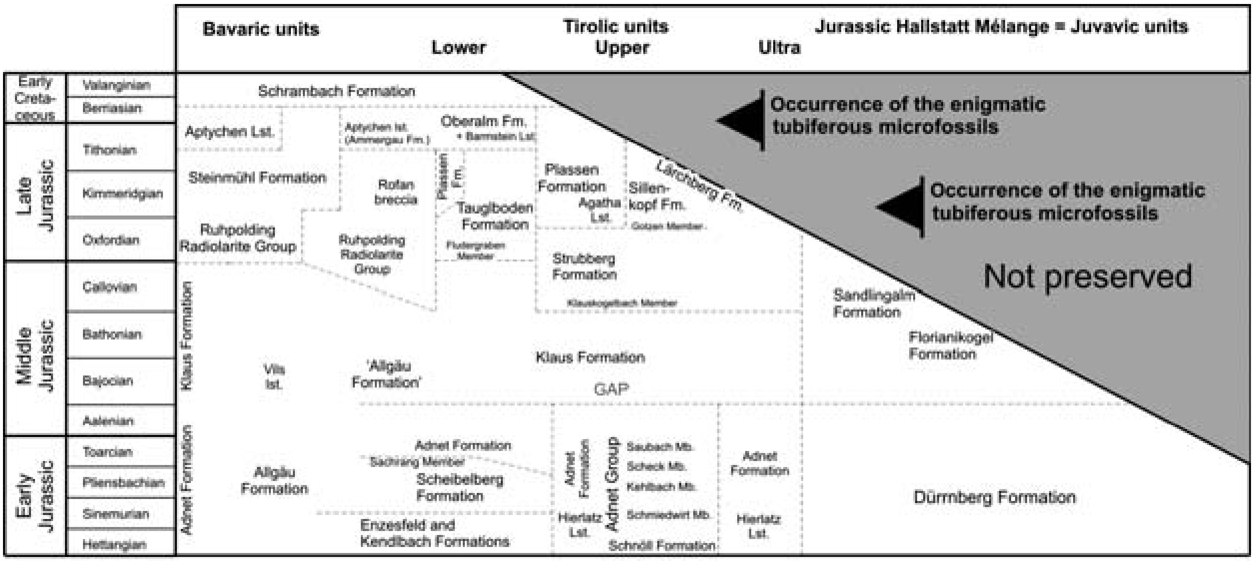

Fig. 2. Stratigraphic table of the Jurassic of the Northern Calcareous Alps with its lateral variations depending on the paleogeographic position (after Gawlick *et al.* 2007).

calcite (except *morphotype*-4) without detectable skeletal elements. Because of the wide morphological range (polymorphism) that obviously reflects intra-specific variability as well as differences at the species and/or genus level (?suprageneric position) and their occurrence in random thin sections, it is rather difficult to describe the specimens in terms of planes of sectioning and to interpret their exact morphology. The most common forms are referred to here as morphotypes 1 to 5.

Morphotype-1. – This is represented by irregular swollen tubes (total length up to 3 mm) showing a more or less flat basal part fixed to the substrate (Fig. 4A–C; cf. pharetronid sponges in Figs 3A, 4B). A thinner, elongate part stretches away from the substrate, but is often also present in the terminal part. Microbial crusts occur as thin micritic linings (Fig. 4A, B) or comparable thick envelopes (Fig. 4C).

Morphotype-2. – The general shape of this small tube type is irregular cylindrical (length: 0.5–1.3 mm; width: 0.15–0.3 mm; Fig. 4D–G). One end maybe tapered and flattened, the other rounded-acute (cf. Fig. 4D, F) and sometimes bent (Fig. 4E).

Morphotype-3. – This type is characterized by more voluminous tubes with one flattened end, the other tapering with an acute-rounded termination (Fig. 4H–J). Irregularly distributed elongated lateral protrusions are conspicuous in longitudinal sections (Fig. 4H–I). Their irregular distribution on both sides clearly indicates that these are not concentric rings or bulges, but individual pustule-like elements. In a single specimen there are different types of protrusions: some are thin and cylindroconically tapering while others are broader with rounded ends.

Morphotype-4. – This type is represented by irregular cylindrical tubes of erect growth with pustule-like elements more regularly distributed along the whole tube and comparably short with respect to morphotype-3 (Figs 3D, 5A–E, 6A). Tube length mostly between 1 and 2 mm, exceptionally up to 5 mm (Fig. 3D), width is 0.2–0.45 mm, at the level of the pustules 0.35–0.85 mm. *Morphotype*-4 occurs either without distinct microbial crusts (Fig. 5A) or more typically surrounded by *Labes atramentosa* Eliášová with the basal part fixed towards the substrate (Fig. 5B–E). The continuation of the tube above the microencruster 'cortex' can be traced in some specimens (Fig. 5B, D). The occurrence of internal sediment (?or relics of the primary hard parts), observable only in this morphotype, could point to partial damage or invasion by a larger opening (Fig. 5D, see also Fig. 6A). A specimen directly comparable to our *morphotype*-4 was figured by Schmid (1996, fig. 110) from the Late Jurassic of Portugal.

Morphotype-5. – The tubes of this type show irregular, sometimes arborescent constrictions (Fig. 5F–H) and/or lateral appendages (Fig. 5G–H), often in gregarious associations (3F). Length of the tube 0.5 to 3 mm.

Microbial crusts and microencrusters

The central tube is herein referred to as the 'core' and the surrounding micritic envelope with tiny tubes as 'crust'. The core typically exhibits crusts of assumed microbial origin (= microbial crusts in the sense of Leinfelder *et al.* 1993). These maybe micritic, fine-peloidal crusts (Fig. 4J) associated with or without

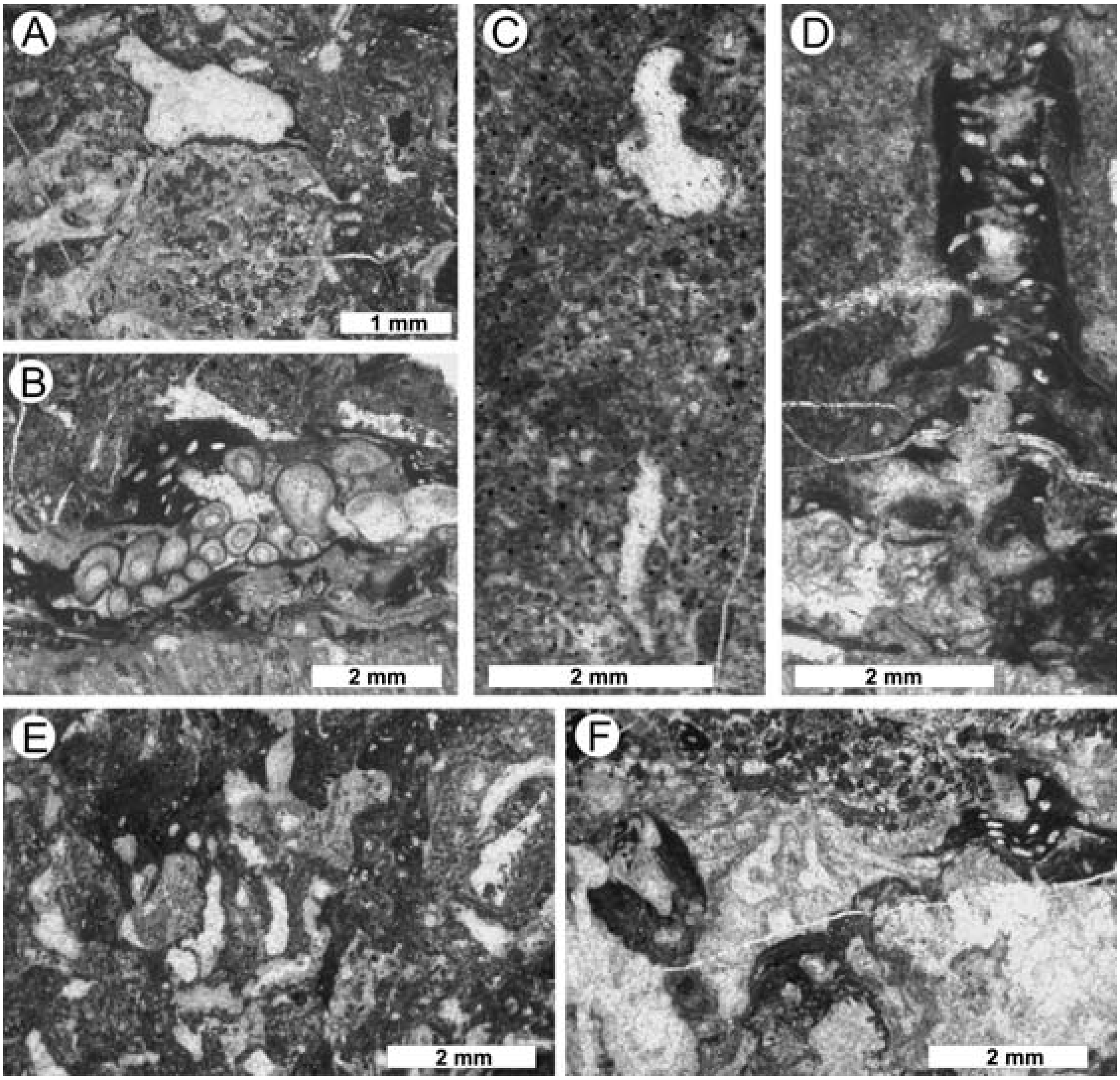

Fig. 3. Late Jurassic fore-reefal to upper slope microfacies containing tube-like organisms. A. Fixed to pharetronid sponge (for magnification see Fig. 4B). B. Switched between serpulids and covered by micritic crust of *Labes atramentosa* Eliášová. C. Irregular shaped tubes with peloidal packstone. D. Cylindrical elongated tube fixed on a coral showing envelope of assumed microbial crusts. E. Numerous tubes with microbial crusts, predominantely of fine-peloidal thrombolitic type. F. Metazoans with tubes fixed by crusts of *Labes atramentosa* Eliášová. A. Mount Krahstein, B. Mount Drei Brüder, C–F. Mount Jainzen.

microencrusters and forming a structure corresponding to the 'layered thrombolite with peloidal microstructure' in the classification scheme of Schmid (1996). Microencrusters with an embedded core belong to the genera *Labes* Eliášová, 1986 (Figs 5B–D, ?E, 6A), *Crescentiella* Senowbari-Daryan *et al.*, 2008 (Fig. 6B), and aff. *Isnella* Senowbari-Daryan, 2007 (Fig. 6C–E), and differ in the dimensions and structure of the micritic sheets and cores (see original references for details). Morphologically very close are *Labes* (Late Jurassic) and *Isnella* (Late Triassic), that according to Senowbari-Daryan (2007, p. 50) should differ, apart from differing stratigraphy, mainly by their dimensions of both 'central hollow' and encrusting tubes, thus, pointing to differences at species rather than genus level (Table 1). Microencruster with tiny pores were designated as *Isnella* aff. *misiki* expressing these uncertainties (Figs 4F and 6C–E); in some specimens there are both tiny and larger tubes (Fig. 6E). Further taxonomic considerations are beyond the scope of the present paper.

For all three taxa mentioned above, a microbial origin (cyanophyts?) was envisaged either in the original descriptions or in recent contributions. Eliášová (1986) regarded the 'major central cavity' as part of *Labes*; for *Isnella* Senowbari-Daryan (2007) assumed the central cavity simply as an empty space resulting from repeated upward coiling of the surrounding tube

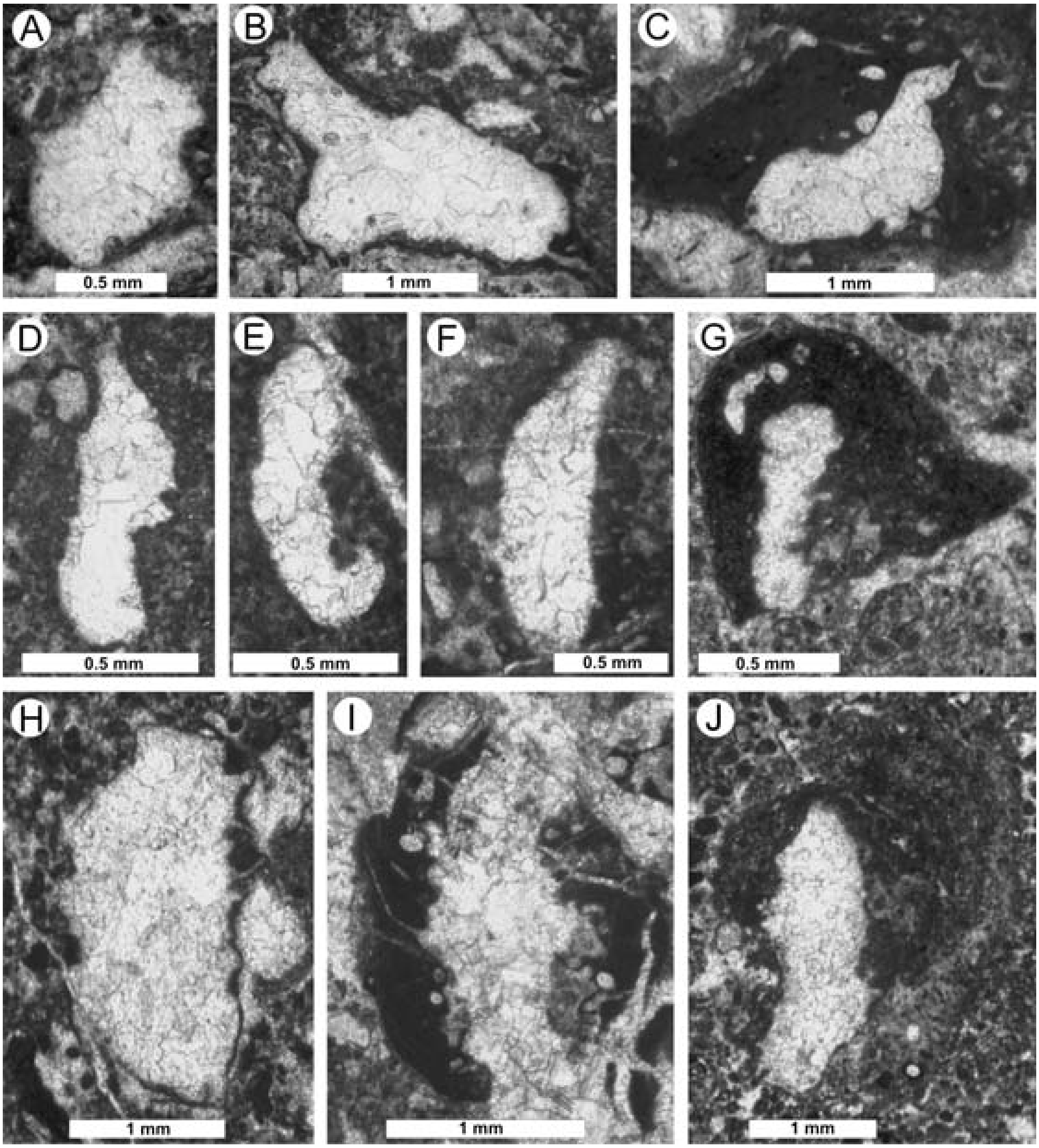

Fig. 4. Thin-section photomicrographs of Late Jurassic tube-shaped microfossils incertae sedis. A–C. *Morphotype*-1 with irregular bulbous shapes fixed to skeletal substrates, e.g. pharetronid sponges (A). Note thin micritic lining (B) and thick microbial crust (C). D–G. *Morphotype*-2, irregular cylindrical with one tapering and rounded (D, F) or bent endings (E). Note thick microbial crust in G. H–J. *Morphotype*-3, with one flattened and one acute ending; lateral pustules and protuberances. Note thick microbial crusts (I–J). A–B. Mount Krahstein, C: Mount Rettenstein, D–F, I–J. Mount Jainzen, G. Mount Trisselwand, H. Mount Drei Brüder (localities see Fig. 1B).

Table 1. Comparison of *Isnella* Senowbari-Daryan, 2007 and *Labes* Eliášová, 1986, both mono-specific taxa. Data of *Labes* are from the Late Jurassic of the Northern Calcareous Alps and between brackets data from Eliášová (1981, 1986).

	Isnella misiki Senowbari-Daryan	*Labes atramentosa* Eliášová	*Isnella* aff. *misiki* Senowbari-Daryan
Morphology	Cylindrical to cupola-shaped	Cylindrical to low conical	
Size	Up to 1.5 mm × up to 6 mm	Up to 3 mm × up to 5 mm	0.5 mm × up to 5 mm
Central diameter	mostly 0.5 mm	0.2–0.85 mm (0.6–1.2 mm)	0.17–0.5 mm
Tube diameter	up to 40 μm	50–150 μm (70–200 μm)	15–70 μm
Stratigraphy	Ladinian–Carnian	Kimmeridgian–Tithonian (?Berriasian)	

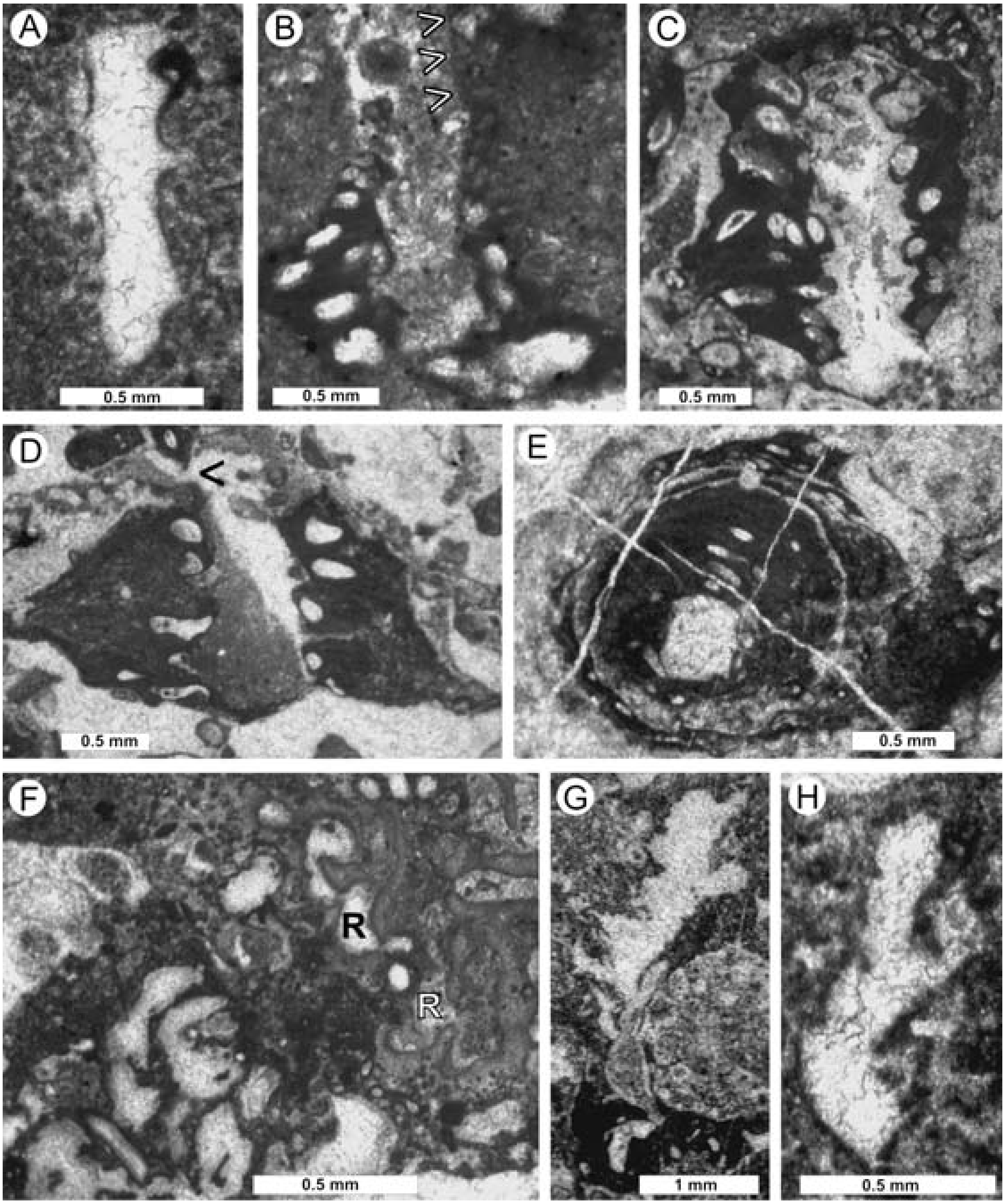

Fig. 5. Thin-section photomicrographs of Late Jurassic tube-shaped microfossils incertae sedis. A–E. *Morphtype*-4, elongated cylindrical tubes with spinose surface texture. Note epibiontic coverage with *Labes atramentosa* Eliášová. Arrows indicate the continuation of the tubes above the basal enveloping. F–H. *Morphotype*-5, irregular to arborescent growth with lateral appendages. Note similar shaped chambers of microencruster *Radiomura cautica* Senowbari-Daryan & Schäfer (R). A, D. Mount Krahstein, C. Mount Trisselwand, B, E–H. Mount Jainzen.

(Fig. 6C–E). A third possibility was discussed by Schmid (1996), noting that the chimney-like growth of '*Tubiphytes*' was similar to the inhalant and exhalant canal system of porifera (see also Brachert 1986). The general interpretation for these '*Tubiphytes*' chimneys (= *Labes atramentosa*), that this peculiar growth type is not just incidental but results from the overgrowth of another organisms in order to take advantages is followed in the present paper (see following discussion). The visible tube sections of *Labes* (width 0.065–0.2 mm) are often wrapped around the embedding central 'core', just between two adjacent

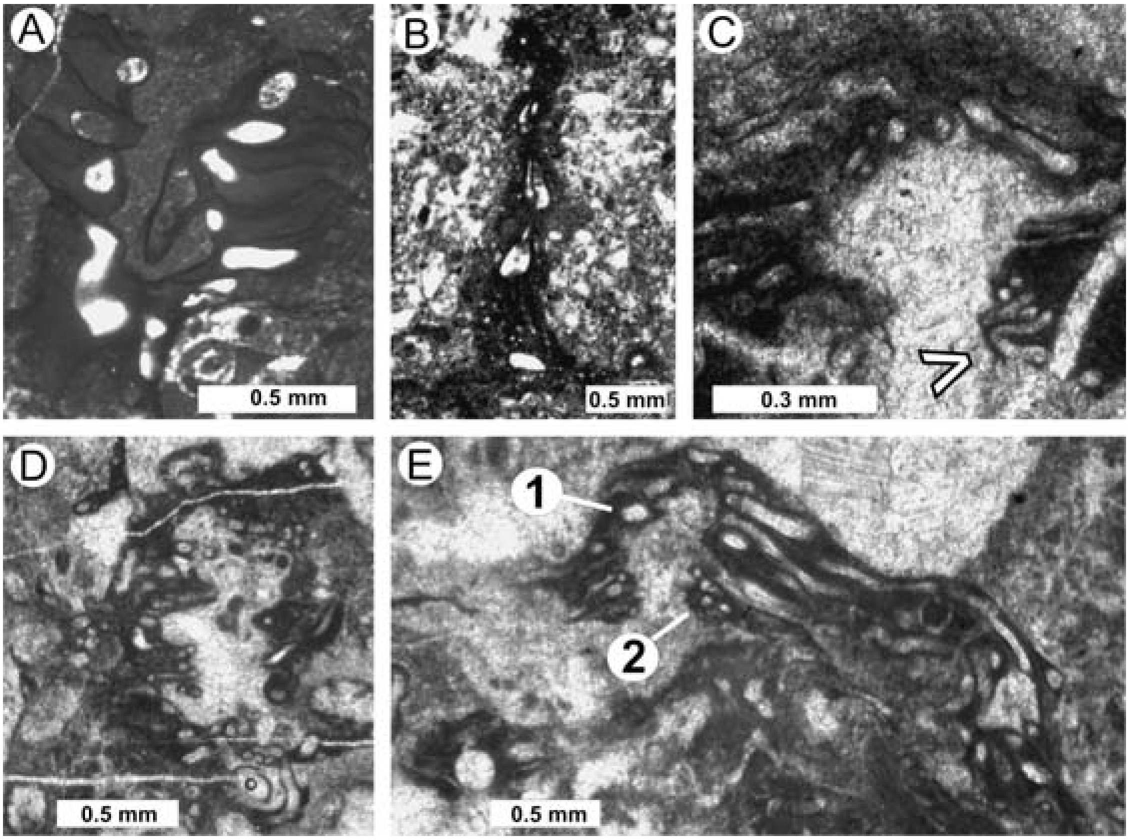

Fig. 6. Microencruster incertae sedis of assumed microbial origin from the Alpine Late Jurassic. A. *Labes atramentosa* Eliášová. B. *Crescentiella morronensis* (Crescenti); here only the micritic portion ('cortex') is interpreted as being microbial in origin (Senowbari-Daryan *et al.* 2008, for details). Note the incorporated fine-detrital material lacking in the crust of *Labes*. C–E. *Isnella* aff. *misiki* Senowbari-Daryan. Note the tubes being finer as in *Labes* showing snail-like enrollment (C: right below). In E there are both small tubes (*Isnella*-type, arrow 2) and larger ones (*Labes*-type arrow 1).

pustules (Fig. 5C, D); in cases of greater distances between the protuberances there maybe two tubes of *Labes*. In cross-sections the tubes of *Labes* also surround the central core in a concentric manner (Fig. 5E). These tube-epibiont constructions can reach heights up to a maximum of 5 mm; in other types the outer micritic crusts of *Labes* become reduced in thickness during growth, resulting in forms that suggest microvolcanoes with basal widths of 2–3 mm (Fig. 5D). The uppermost part of the embedded tubes obviously were not encrusted (Fig. 5B, D); the 'overall' crusts of the specimen shown in Figure 5C is likely due to oblique sectioning.

There seems to exist special relationships between certain microencrusters and tube morphotypes with the surface morphology obviously impacting the epibiont coverage. For example, the occurrence of *Labes atramentosa* and *Isnella*-type crusts have shown to preferentially encrust spinose textured tubes, most typically *morphotype*-4 but also *morphotype*-3. The spinose surface obviously was advantageous for enhanced tube coverage. Growth seems to have initiated in a manner relatively parallel to the tubes surroundings, followed by enlargement and final broadening of the base. In this way, better fixing to the substrate independent from the tube was obtained and possible acted as nucleus for larger micrite mounds. Tubes of *morphotype*-2 with a smoother surface show strong thrombolitic crusts (Fig. 4D, E) and in rare cases *Isnella*-type crusts also occur (Fig. 4F). Arborescent-shaped tubes usually do not exhibit distinct microencruster envelopes, but commonly display a thin covering of more densely packed peloids than the surrounding sediment (Fig. 5G–H) or gregarious associations of thrombolitic crusts (Fig. 5F).

Interpretation of the tubes

The morphological features (e.g. spinose surface, differences in opposed tube endings) together with common tube-specific epibionts reveal a higher grade of organization for these unknown organisms, thus excluding an abiogenic or ichnological origin such as worm-like burrows (cf. Elliott 1980; fig. 8F *in* Riding & Thomas 2006).

Looking at elongated variously-shaped organisms with or without protrusion on the surface, a possible sponge origin (sponge mummies) is here favoured. In terms of sponge description (see Hooper 2000, for glossary) the pustule-like elements of the 'tubes' are likely to represent fistules, combined with pores (exhalant or inhalant) of the aquiferous system. These forms correlate well with those of sponges, for instance massive-lobate (*morphotype*-1), ovate (*morphotype*-2), tubular or columnar erect, cylindrical, club-shaped (*morphotype*-4) or arborescent-bifurcate branching (*morphotype*-5). In addition, *morphotypes*-3 and -4 can be attributed to the surface structures 'fistulose', 'conulose' or with fistules (see Hooper 2000, for details). The supposed tube opening (opposite to the attached part) could be a terminal osculum and the pustules lateral oscula. With respect to the outer surface morphology or epibiont moulding, a cross-reference can be drawn to extant sponges where a distinct host specificity of sponge-associated bacteria was evidenced (e.g. Taylor *et al.* 2004). In conclusion, the tubes generally compare with sponges morphologically, and also in the interpretation of the mode of life, as discussed below. However, we cannot exclude that the different morphotypes described herein belong to different species/genera or perhaps to different groups of organisms.

Mode of life of the tube-microbial consortium

In the fore-reefal boundstones, microencrusters of the group *Labes–Isnella–Crescentiella* exhibit a maximum occurrence as crusts around the reported 'tubes'. This distribution and the aforementioned host-specificity are regarded as not only incidental but also as providing evidence of a special ecological interaction/relationship between the two groups involved. It is also plausible that encrustation of the tubes happened during the life-time of the sponges (compare also Schmid 1996, p. 190). Normally there are enough elongated skeletal remains for fixation in the same palaeoenvironment. Our assumption of a sponge nature of the tubes enveloped by *Labes* and other types of microbial crusts is in accordance with Brachert (1986) and Schmid (1996), indicating that these grew around the pores (exhalant/inhalant) of the sponge's aquiferous system. Brachert (1986, for details) discussed different modes/types of diagenetically controlled siliceous sponge preservation with cemented moulds (mummies) (type C–E) that correspond to our findings. Within this field, the central tube organisms performed a passive 'task' simply acting as the substrate for the actively encrusting microorganism. As sponges are organisms that filter food particles/nutrients from seawater, it is likely that the crustose epibionts participated in this activity. How greatly the sponge capability of the intake/uptake of nutrients was negatively influenced is unclear. In this manner, the surrounding tuberculated/fistulated tubes can be interpreted as a strategy for direct participation in the gathering of nutrients. The core-forming biota benefited in turn by protection from predation by the coverings and by better fixation to the substrate, thereby gaining more stability against environmental hazards (cf. storm waves) enhancing survival. Fixation by the crusts must have been a very rigid construction, since we never observed isolated broken specimens. The observed encrustations as well as the dark rim surrounding the tube (e.g. Figs 4F and 6A) could point to the existence of a former skeleton (?aragonite, ?amorphous silica) that became totally recrystallized during diagenesis. The existence of siliceous sponges in this environment, for instance, is indirectly proven by the occurrence of siliceous rhaxellid/rhaxelloid sponge microscleres in the Late Jurassic fore-reefal limestones of the NCA (Schlagintweit *et al.* 2007). Interestingly, the occurrence of *Reophax*? *rhaxelloides*, which is composed of spherical sponge microscleres ('rhaxes'), is bordered with tubes in the same localities. Another possibility would be that these tubes were originally only composed by soft tissue (?soft sponges).

Specimens without enveloping crusts may occasionally be observed dispersed in the sediment (Fig. 5A). We conclude that both 'core'- and 'crust'-forming biota benefitted from this specialized association pointing to mutualism rather than to commensalism (Boucher *et al.* 1982). It is important to mention that the Alpine settings are different from those of the Late Jurassic outer ramp deposition of siliceous sponge facies at the European margin (e.g. Matyszkiewicz 1997; Krautter 1998), where these tube-microbial crust constructions also occur in a presumably deeper water and less agitated environment (Brachert 1986; Schmid 1996). Here, the advantage of the moulded sponges is not directly evident. Perhaps they benefited from the metabolic products of the microencrusters but this is unclear.

Similar-shaped tubes of unknown systematic position are also reported from Middle to Late Triassic reefal carbonates (Fig. 7). The re-appearance of such structures (including *Isnella*-type crusts) in the Late Jurassic with a gap of roughly 50 Ma could therefore be discussed as holdover taxa, refugia species or an example of the Lazarus effect (e.g. Stanley 1998; Wignall & Benton 1999).

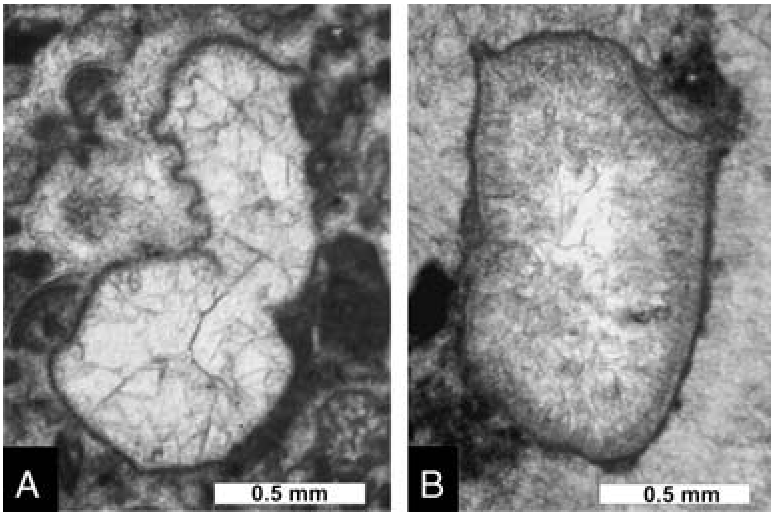

Fig. 7. A–B. Tubes incertae sedis from Middle Triassic reefal limestones of the Southern Alps of Italy. Note that the pustules of the specimen shown in A are ring-like, passing around the tube.

Conclusions

Late Jurassic reefal platform margin carbonates contained not only the typical associations of corals, stromatoporoids and diverse microencrusters but also tube-like organisms of unknown systematic position associated with microbial crusts. The enveloping of the microencruster (biomuration) enabled the preservation of the tubes hollow that would otherwise perhaps have been lost during taphonomy, making palaeoecological reconstructions and syntheses difficult. For the tube-like organisms, an interpretation as a mutualistic and non-parasitic biological interaction between sponges and microbial communities is favoured; however, more details are needed to assess the biological nature of these enigmatic structures more precisely. These substrate-fixed tube-crust constructions are a characteristic element in the well-agitated fore-reefal carbonate facies of the Late Jurassic Plassen Carbonate Platform in the Northern Calcareous Alps. In ramps along the northern European margin of Alpine Tethys, such structures are also recorded, but from a deeper-water depositional setting of the siliceous sponge facies that is lacking in the Northern Calcareous Alps. Future micropalaeontological investigations should allow a better refinement of existing Late Jurassic general reef types, reef zonations and reefal biocoenoses also on a microscale.

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