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Disaster microconchids from the uppermost Permian and Lower Triassic lacustrine strata of the Cis-Urals and the Tunguska and Kuznetsk basins (Russia)

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Abstract

We describe aggregative microconchid (Lophophorata) tubes from the uppermost Permian (upper Changhsingian) and Lower Triassic (Olenekian) lacustrine and fluvial strata of the Tunguska and Kuznetsk basins and the southern Cis-Urals, Russia. These attach to clam shrimp carapaces, bivalve shells, terrestrial plant fragments and a horseshoe crab head shield, and also form their own monospecific agglomerations. Planispiral tubes of a wide size range (0.1–2.5 mm) create dense settlements on these firm substrates, which likely comprise multiple generations of the same species. These finds confirm that this extinct lophophorate group was inhabiting non-marine continental basins during latest Permian and earliest Triassic time, when they were major suspension feeders in such limnic ecosystems. Microconchids dispersed extensively and rapidly in the aftermath of the Permian–Triassic mass extinction into both marine and continental basins at low and moderately high latitudes, which were notably different in salinity, temperature, depth and redox conditions. This confirms that small lightly calcified microconchids were a genuine disaster eurytopic group, whose expansion may have been promoted by low predator pressure and low competition for substrate.

1. Introduction

Encrusting tubicolous microconchids are a Late Ordovician – Middle Jurassic group of mostly marine taxa. On the basis of their regularly coiled calcareous tubes, microconchids, including Permian and Triassic forms, were variously classified as either the polychaete tubeworm *Spirorbis*, spirorbids as a whole, serpulids, tubicolous worms or sometimes microgastropods (e.g. Gall, 1971; Peryt, 1974; Kelber, 1987; Adachi *et al.* 2004; Vaslet *et al.* 2005; Kukhtinov, 2017). However, in-depth studies of the tube ultrastructure and morphology proved that they were neither polychaetes nor molluscs, but resembled most closely the tentaculitoids, together with which the order Microconchida forms the class Tentaculita, probably an extinct lineage of the lophophorates (Weedon, 1991; Taylor & Vinn, 2006; Taylor *et al.* 2010; Vinn, 2010). Compared with serpulids, which possess aporose tubes open at both ends and chevron-shaped growth increments in their wall structure, microconchids had a closed bulbous protoconch at the proximal end of the tube and a foliated wall fabric traversed by pseudopunctae and pores similar to brachiopods and bryozoans (Taylor & Vinn, 2006; Vinn *et al.* 2008; Zatoń & Olempska, 2017).

Microconchids appeared in the Late Ordovician seas and began colonizing continental settings probably as early as during the Early Devonian Epoch, populating a wide range of environments in brackish and fresh waters (Taylor & Vinn, 2006; Caruso & Tomescu, 2012; Zatoń *et al.* 2012, 2016b; Zatoń & Peck, 2013; Matsunaga & Tomescu, 2017). Recently, the autochthonous origin of brackish- and fresh-water microconchids has been challenged and their presence in such settings has been explained by invasions of marine waters that brought into continental lowland aquatic systems detached tubes or short-term surviving larvae during storm surges and tsunamis (Gierlowski-Kordesch & Cassle, 2015; Gierlowski-Kordesch *et al.* 2016).

Here we describe microconchids from lacustrine and fluvial settings in the uppermost Permian strata of the Tunguska and Kuznetsk basins and the Lower Triassic deposits of the southern Cis-Urals (Russia). We further summarize palaeoecological and palaeobiogeographical data on latest Palaeozoic and earliest Mesozoic microconchids to interpret these new occurrences as unique disaster eurytopic survivors of the Permo-Triassic mass extinction (Fig. 1).

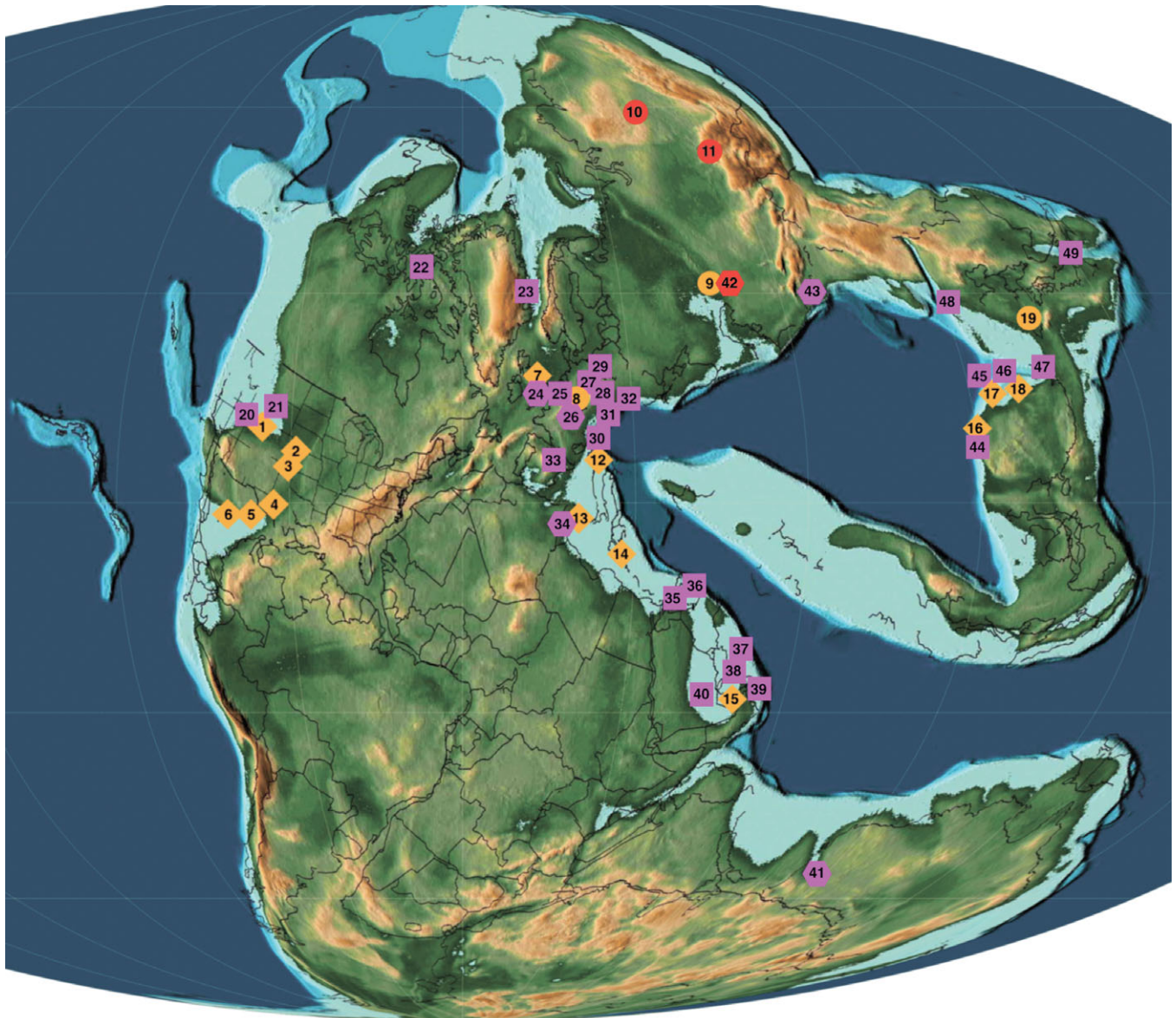


Fig. 1. (Colour online) Early Triassic, Olenekian (250 Ma) palaeogeography (generated from <https://www.earthbyte.org/paleomap-paleoatlas-for-gplates/> with GPlates 2.1.0) showing Permian and Lower–Middle Triassic localities with microconchids (locality numbers correspond to those in Table 2). Orange rhombs – Permian marine localities; orange circles – Permian lacustrine localities; violet squares – Triassic marine localities; violet hexagons – Triassic lacustrine localities; red symbols – lacustrine localities under discussion (10 – uppermost Permian Tunguska Basin, 11 – uppermost Permian Kuznetsk Basin, 42 – Lower Triassic southern Cis-Urals; Russia).

2. Geological background

2.a. Uppermost Permian Tunguska Basin

The Tunguska Basin of the Siberian Platform hosts the Permian–Triassic Traps large igneous province (LIP), the eruption of which caused the most severe mass extinction known. Trap formation started at the end of the Permian Period from initial volcanic ejections leading to volcanic ash (tuff) deposition, followed by an increasing volcanic activity and the emplacement of mafic sills and dykes, and finally by the vast lava floods of dominantly basaltic compositions that bracket the Permian–Triassic boundary interval (Fedorenko & Czamanske, 1997; Reichow *et al.* 2009; Ivanov *et al.* 2013). The lowermost Triassic volcanoclastics in this sequence contain a number of combusted woody fragments and char particles embedded in the volcanoclastic matrix (Elkins-Tanton *et al.* 2020).

The strata bearing microconchids are exposed along the middle reaches of the Nizhnyaya Tunguska River (50–90 km east of the settlement of Tura, Krasnoyarsk region), which crosses the flood basalt plateau in its southern area. These beds are a part of the terrestrial volcanic-siliciclastic Bugarikta Formation, the deposition of which corresponds to the interval immediately preceding the major basalt flooding event (Fig. 2, sites 1–4, Table 1). Going west and downstream along the Nizhnyaya Tunguska River, these exposures are at Degigli (64° 01' N, 102° 01' E), Anakit (64° 07' N, 101° 52' E), Khungtukun (64° 10' N, 101° 42' E) and Nizhnyaya Lyulyuikta (64° 07' N, 101° 15' E). The Bugarikta Formation conformably overlies the Upper Permian Uchami Formation here, which consists primarily of massive coarse-grained volcanic tuffs and xenomorphic tuffs and, in places, agglomerated unsorted volcanoclastic breccia, and is overlain by the dominantly basaltic Nidym Formation. The Bugarikta Formation is 50–270 m in

Table 1. Lithostratigraphic chart of the Permian–Triassic boundary strata in the Cis-Urals and the Tunguska and Kuznetsk basins of Central Siberia (Saks *et al.* 1981; Krasnov *et al.* 1982; Kazakov *et al.* 2002; Tverdokhlebov *et al.* 2005; Knyazev *et al.* 2013; Kukhtinov *et al.* 2016); microconchid-bearing units in bold; the Ryaboy Kameshek, Kedrovka, Barsuch'ya and Tarakanikha subformations compose the Mal'tsevo Formation

Series	Stage	Formation/subformation		
		Southern Cis-Urals	Tunguska Basin, Nizhnyaya Tunguska River	Kuznetsk Basin, Babiy Kamen'
Lower Triassic	Olenekian	Petropavlovka		
		no deposits	no deposits	no deposits
	Induan	Kzylsay		
		Staritsa		
Upper Permian (pars)	Changhsingian	Kopanskiy	Kochechumo	Yaminskaya
		no deposits	Nidym 251.901±0.061 ^a	Sosnovaya 251.9±0.7 ^b Ryaboy Kameshek
		Kul'chumovo	Bugarikta	Kedrovka 252.3±0.6 ^b
			Uchami	
			no deposits	Barsuch'ya
			Tutonchana 252.24±0.12 ^a	Tarakanikha
			Gagariy Ostrov	Taylugan
			no deposits	Degali

^aGeochronological dates (Ma; Burgess & Bowring, 2015).

^bGeochronological dates (Ma; Svetlitskaya & Nevolko, 2016).



Fig. 2. (Colour online) Map of Russia indicating sections discussed here: (1–4) uppermost Permian (Changhsingian) (1) Degigli, (2) Anakit, (3) Khungtukun and (4) Nizhnyaya Lyulyuikta sections of the Tunguska Basin, Krasnoyarsk region; (5) uppermost Permian (Changhsingian) Babiy Kamen' section of the Kuznetsk Basin, Kemerovo region; (6) Lower Triassic (Olenekian) Petropavlovka III section, southern Cis-Urals, Orenburg region. Base map source: https://en.wikipedia.org/wiki/Wikipedia:WikiProject_Geographical_coordinates.

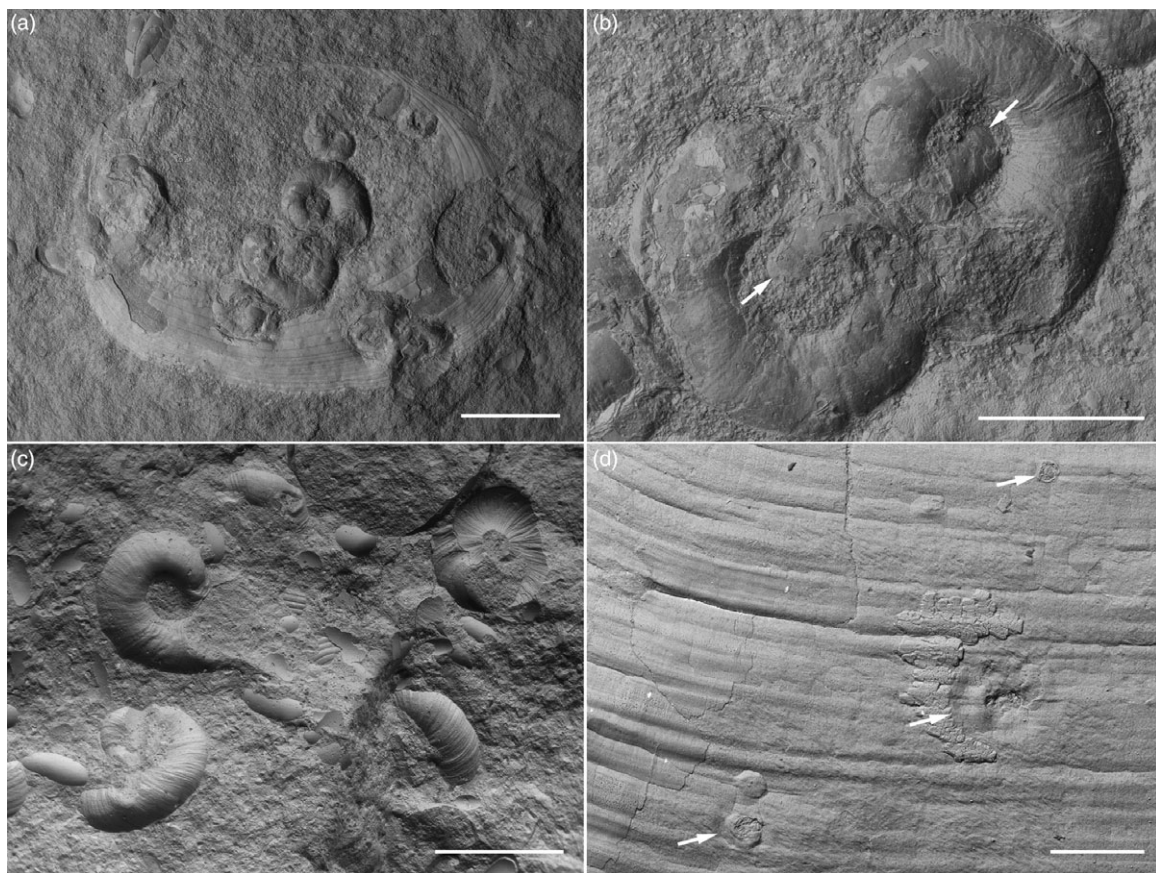


Fig. 3. Microconchid tubes from the uppermost Permian (Changhsingian), Siberia, Russia; ESEM (BSE). (a) PIN 2716/3, aggregation encrusting spinicaudatan carapace, Bugarikta Formation, Deggli section, Tunguska Basin. (b) Detail of (a), two tubes showing embryonic chambers (arrowed) and microsculpture. (c) PIN 2402/33 packstone consisting of microconchid tubes (mostly) with groove-like attachment scar (bottom left), ostracod carapaces and charophycean gyrogonites, Bugarikta Formation, Nizhnyaya Lyulyuikta section, Tunguska Basin. (d) PIN 4887/822, attachment scars of three microconchids (arrowed) encrusting a bivalve shell, Mal'tsevo Formation, Babiy Kamen' section, Kuznetsk Basin. Scale bars: (a, c) 1 mm; (b) 0.5 mm; and (d) 0.2 mm.

thickness, consisting of variegated volcanic-sedimentary medium- to coarse-grained volcanic ash-rich tuffite, medium- and coarse-grained tuff, grey and dark-brown thin-bedded fine- to coarse-grained siltstone and fine-grained sandstone, with lenses of siltstones consolidated by a calcareous cement; taxite-type basalt sills are interbedded with the other lithologies (Saks *et al.* 1981; Sadovnikov & Orlova, 1995; Sytchevskaya, 1999; Mogutcheva & Krugovykh, 2009).

The macroflora and miospore assemblages characterizing the entire Bugarikta Formation have a transitional Permian–Triassic appearance: they lack cordaitaleans and yield mostly ferns, peltasperms and conifers with less common sphenophytes (Prinada, 1970; Krugovykh, 1987; Mogutcheva, 1987, 2016; Mogutcheva & Krugovykh, 2009; Sadovnikov, 2015a, b). *Cordaitina* pollen grains, which were earlier attributed to cordaitaleans (Romanovskaya *et al.* 1973), possess a different exin ultrastructure and therefore do not provide evidence for the presence of the cordaitaleans in transitional Permian–Triassic strata of the Tunguska and Kuznetsk basins (Zavialova *et al.* 2004). In addition to terrestrial vascular plant remains, charophycean gyrogonites are extremely common together with various shelly fossils, within the grainstone–packstone lenses in the Khungtukun and Nizhnyaya Lyulyuikta sections (Fig. 3c). Siltstone and sandstone beds from the localities under discussion contain a rich assemblage of freshwater clam shrimps or spinicaudatans (Anakit and Khungtukun;

Sadovnikov & Orlova, 1995; Sadovnikov, 2008; Figs 3a, 4a), ostracods (Anakit, Khungtukun and Nizhnyaya Lyulyuikta; Sadovnikov, 2008; Fig. 3c), a rich insect fauna (Anakit, Khungtukun and Nizhnyaya Lyulyuikta; Aristov *et al.* 2013), neopterygian fishes (Berg, 1941; Sytchevskaya, 1999) and the temnospondyl amphibian *Tungussogyrinus bergi* (Anakit and Nizhnyaya Lyulyuikta; Efremov, 1939; Shishkin, 1998).

In the regional stratigraphic chart (Saks *et al.* 1981) and in a number of palaeontological publications dealing with fossil flora and fishes, these strata are ascribed to the Lower Triassic (e.g. Mogutcheva, 1987; Sytchevskaya, 1999; Mogutcheva & Krugovykh, 2009). Despite the fact that these strata occupy a higher stratigraphic position than the presumable interval corresponding to the mass extinction, which eliminated the Permian cordaitalean flora, and also than the base of the coal gap (reviewed by Retallack *et al.* 1996), they lack any typical Triassic elements. Even their most specific genera, such as the fish *Evenkia* and the conifer *Quadrocladus*, are known from the Upper Permian strata of Europe and other regions (Aristov *et al.* 2013; Sadovnikov, 2015a, b; Bajdek *et al.* 2016; Bernardi *et al.* 2017; Blumenkemper *et al.* 2018; Karasev *et al.* 2018). Additionally, based on the high-precision uranium/lead (U/Pb) chemical abrasion – thermal ionization mass spectrometry geochronology of the northern Maymecha–Kotuy area within the Tunguska Basin (Burgess & Bowring, 2015) and on its correlation with the

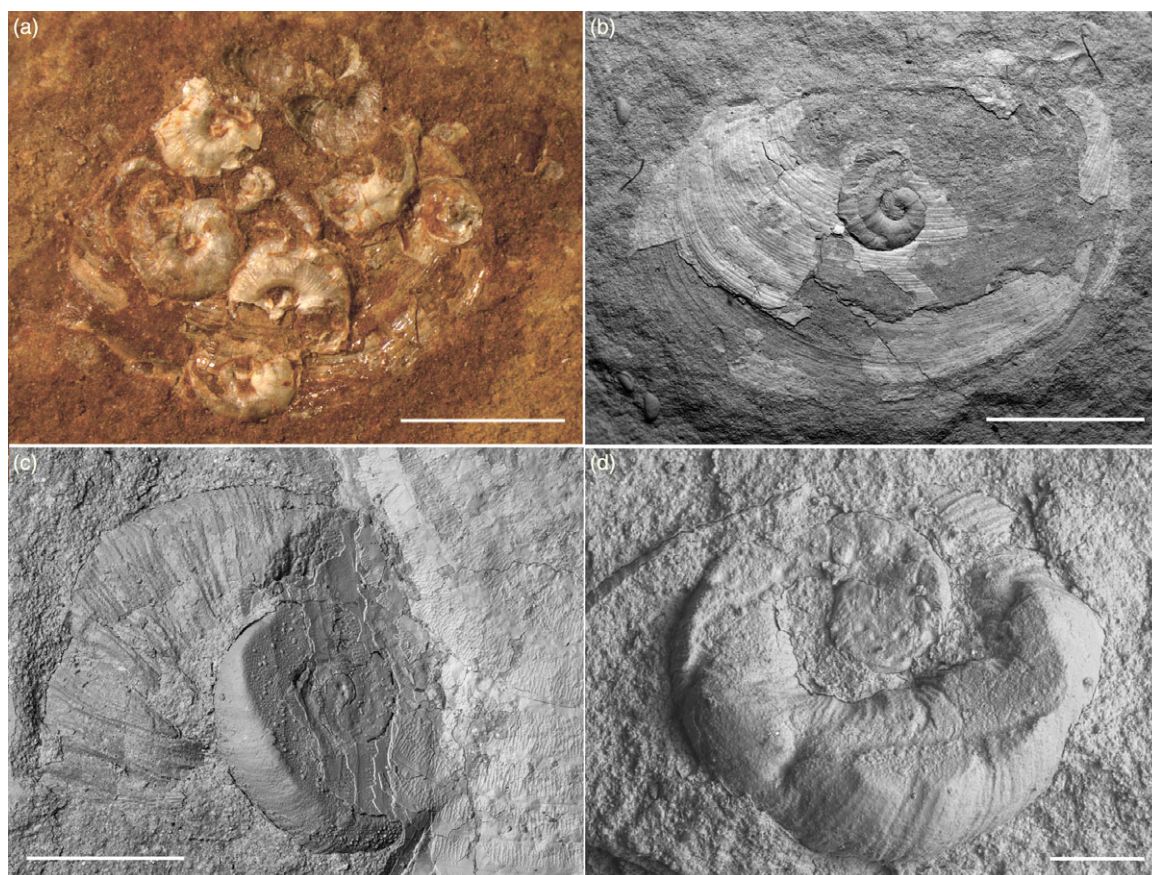


Fig. 4. (Colour online) Microconchid tubes encrusting spinicaudatan carapaces from the Bugarikta Formation, uppermost Permian (Changhsingian), Anakit section, Tunguska Basin, Krasnoyarsk region, Russia. (a) PIN 2362/27, large aggregation of mature individuals. (b) PIN 3061/27, ESEM (BSE), large individual. (c) PIN 5381/344, ESEM (BSE), showing lower attachment area and microsculpture, a spinicaudatan carapace with striated ornamentation is on the right. (d) PIN 5381/350a, ESEM (BSE), showing attachment area, bulbous embryonic chamber and microsculpture. Scale bars: (a, b) 2 mm; (c) 0.5 mm; and (d) 0.2 mm.

Nizhnyaya Tunguska River area (Kazakov *et al.* 2002; Table 1), the Bugarikta Formation occurs below the geochronologically dated 251.902 ± 0.061 Ma base of the *Hindeodus parvus* conodont Zone, which defines the Permian–Triassic boundary in marine facies (Kozur & Weems, 2010; Sadovnikov, 2015a, b, 2016). These biostratigraphic and geochronological constraints restrict the age of the microconchid-bearing strata of the Tunguska Basin to the uppermost Permian Changhsingian Stage (Table 1).

2.b. Uppermost Permian Kuznetsk Basin

The Kuznetsk Basin is a vast late Palaeozoic–Mesozoic depression occupying the NW part of the Altay–Sayan Foldbelt of southern Siberia (Kemerovo region), which was superimposed onto an older terrane that was accreted to the main Siberian (Angara) Craton by the Silurian Period (Sennikov, 2003; Cocks & Torsvik, 2007; Fig. 2, site 5). As in the Tunguska Basin, substantial coals were deposited here during Permian time under northern temperate paralic non-marine conditions. This accumulation was interrupted by a basalt trap eruption dated at 252.9 ± 0.4 – 251.9 ± 0.7 Ma (based on plagioclase $^{40}\text{Ar}/^{39}\text{Ar}$). Geochemical and petrological features, palaeomagnetic characteristics and the age coincidence suggest a common LIP genetic source of Kuznetsk Basin lavas with those of the Tunguska Basin (Kazansky *et al.* 2005; Reichow *et al.* 2009; Buslov *et al.* 2010; Svetlitskaya & Nevolko, 2016). In the Kuznetsk Basin, radiometric ages were obtained for basaltic

andesite and trachyandesite units and basalt sills occurring within the uppermost Permian (Changhsingian) Mal'tsevo Formation. The formation is subdivided into four subformations (in ascending order: the Tarakanikha, Barsuch'ya, Kedrovka and Ryaboy Kameshek) and composed of a well-expressed cyclic alternation of sandstone (with conglomerate lenses), siltstone, mudstone and argillaceous marlstone formed in lacustrine and fluvial environments and containing a significant proportion of pyroclastics (Neuburg, 1936; Vasil'eva, 1962; Vladimirovich *et al.* 1967; Kazakov *et al.* 2002). The Mal'tsevo Formation is underlain by the Upper Permian continental coal-bearing siliciclastic Taylugan Formation and overlain by the Lower Triassic non-marine volcanic-siliciclastic Sosnovaya Formation (Table 1). The key section, Babiy Kamen' ($54^{\circ} 23' \text{ N}$, $87^{\circ} 32' \text{ E}$), occurs on the right bank of the Tom' River (75 km NNE of the town of Novokuznetsk); the microconchids are found in the upper Kedrovka Subformation, which is 75–150 m thick. This unit consists of massive and laminated mudstone, massive, laminated and ripple cross-stratified siltstone and sandy tuff, and is suggested to be deposited in braided river channel systems and low-energy long-lived lakes within a vast fluvial floodplain (Neustrueva & Bogomazov, 1987; Shcherbakov *et al.* 2002; Davies *et al.* 2010).

In addition to microconchids, the Kedrovka Subformation yielded rich faunas of freshwater ostracods (Kukhtinov & Neustrueva, 1986); spinicaudatans (Davydov *et al.* 2019); the bivalve *Utschamiella* (Silantiev *et al.* 2020; Fig. 3d); various insects

(Shcherbakov, 2008c; Aristov *et al.* 2013); gastropods; millipedes; scales of juvenile Acropholidae, Elonichthyidae and Palaeoniscidae actinopterygian fishes; tetrapod bones (Neuburg, 1936; Shcherbakov *et al.* 2002); and macrofloras consisting of the sphenophyte *Neokoretrophyllites*, the ferns *Cladophlebis*, *Katasiopteris*, *Kedroviella* and *Kchonomakidium*, the peltasperm *Lepidopteris*, the putative ginkgophyte *Rhipidopsis* and the conifer *Quadrocladus* (Neuburg, 1936; Betekhtina *et al.* 1986; Mogutcheva & Krugovykh, 2009; Karasev, 2015). The palynoflora demonstrates the dominance of a fern-ginkgophyte vegetation (Romanovskaya *et al.* 1973). Based on the similarity of their faunal and floral fossil assemblages, the Kedrovka and Ryaboy Kameshek subformations are correlated with the Uchami and Bugarikta formations of the Tunguska Basin (Kukhtinov & Neustrueva, 1986; Kazakov *et al.* 2002; Mogutcheva & Krugovykh, 2009; Aristov *et al.* 2013; Davydov *et al.* 2019; Table 1). Similarly, these strata are assigned to the Lower Triassic in the regional stratigraphic chart (Saks *et al.* 1981), although geochronology supports their Changhsingian age (Svetlitskaya & Nevolko, 2016; Table 1).

2.c. Lower Triassic Petropavlovka Lagerstätte

The fossiliferous Permian–Triassic succession of the Cis-Urals is well known for diverse fossil tetrapods and sections that allow for a detailed study of changes in climate, landscapes, vegetation, and insect and vertebrate communities across the Permian–Triassic boundary (Ochev & Shishkin, 1989; Ochev & Surkov, 2000; Shishkin *et al.* 2000; Benton *et al.* 2004; Gomankov, 2005; Shcherbakov, 2008a; Benton & Newell, 2014). During the Early Triassic Epoch (Olenekian), orogenic movements were renewed in the Ural Mountains and the Peri-Caspian Depression was inundated by a transgression of the Palaeotethys, leading to increased rates of siliciclastic deposition in the Cis-Urals (Tverdokhlebov, 1987). In the Cis-Ural Trough and on the nearby southeastern slope of the Volga-Ural Anteclise, a vast lacustrine-deltaic floodplain was formed, bordering the northern Peri-Caspian marine basin of the Palaeotethys (Fig. 2, site 6).

The Petropavlovka area was a part of this floodplain that accumulated grey and reddish-grey siliciclastics, mostly a rhythmic alternation of cross-laminated coarse-grained polymictic sandstone, parallel-bedded fine-grained sandstone, reddish-yellow, reddish-brown or grey subparallel-layered clay, siltstone and fine-grained clayey sandstone, reaching 400–800 m in total thickness (Tverdokhlebov, 1987; Shishkin *et al.* 1995). Conglomerate lenses are also common containing igneous and metamorphic pebbles originating in the Urals. Mud cracks and rhizoliths are generally restricted to the finer parallel-bedding lithologies; coarser sediments represent alluvial deposits while finer lithologies constitute shallow-water lacustrine deposits (Tverdokhlebov *et al.* 2007). These facies characterize delta floodplain and delta front complexes of the Petropavlovka Formation. This unit disconformably overlies the lower Olenekian coarse-grained Kzylsay Formation, and is disconformably overlain by the Middle Triassic siliciclastic Donguz Formation (Tverdokhlebov, 1967, 1987; Table 1).

The Petropavlovka Formation itself is ascribed to the upper Olenekian strata based on the *Parotosuchus* tetrapod fauna, the lungfish *Ceratodus multicristatus*, miospore assemblages rich in *Densoisporites nejburgii* associated with the lycophyte *Pleuromeia*, and magnetostratigraphy (Shishkin *et al.* 1995; Tverdokhlebov *et al.* 2003; Novikov, 2018). One of its key sections

(locality Petropavlovka III, bed 43; Tverdokhlebov, 1967, p. 119) occurs along the Sakmara River near the village of Petropavlovka c. 45 km NE of the town of Orenburg (coordinates 52° 02' N, 55° 38' E) and consists of fossiliferous coarse-grained red beds containing a metre-thick lens of grey fine-grained micro-wavy to parallel-laminated polymictic siltstone to sandstone. Plant and animal fossils are not restricted to certain bedding planes but are randomly distributed in the rock, thus preserving some three-dimensionality. Such a sediment probably accumulated in an ephemeral pond during a flood event. The lens contains abundant plant megafossils including sphenophytes (*Equisetites* sp. and *Neocalamites* sp.) and gymnosperms – *Carpolithus* sp. seeds and *Voltziopsis* sp. conifer ovuliferous scales (Dobruskina, 1994; Shishkin *et al.* 1995). The fossil vertebrate coenosis represented by the lungfish *Ceratodus* (Minikh & Minikh, 1997) and temnospondyl amphibians (Shishkin *et al.* 1995; Novikov, 2018) is typical of the entire formation. Red beds yield spinicaudatans and ostracods as well as crayfish burrows (Tverdokhlebov, 1967; Sennikov & Novikov, 2018).

During the 2018 and 2019 field seasons, numerous insect wings and fragments including various roaches, beetles and hemipterans, rare dragonflies, grylloblattids and orthopterans, as well as tomiulid millipedes, horseshoe crabs, microconchids and a micro-drile oligochaete worm, were excavated along with additional terrestrial plant remains (*Sphenopteris* sp. pinnules and lycophyte fragments), ostracods, clam shrimps and fish scales (Hannibal & Shcherbakov, 2019; Shcherbakov *et al.* 2019, 2020).

3. Methods

Microconchid images were obtained with a Leica M165C stereomicroscope coupled to a Leica DFC425 digital camera. High-resolution images were taken on TESCAN VEGA variable-pressure and environmental scanning electron microscope (ESEM) using backscattered electron (BSE) and secondary electron (SE) detectors at the Borissiak Palaeontological Institute, Russian Academy of Sciences (PIN RAS). Elemental analysis of uncoated and unpolished samples of both fossils and adjacent matrices was performed with a quantitative energy-dispersive spectrometer (EDS) X-ray Inca coupled to the TESCAN VEGA SEM, at an accelerating voltage of 20 keV, in PIN RAS. All samples are housed in PIN RAS, under collections numbers 2362, 2402, 2716, 3061, 4887, 5381 and 5640.

4. Results

4.a. Late Permian microconchids of the Tunguska and Kuznetsk basins

Several hundred complete or partially preserved microconchid tubes were observed, either attached to the outer surface of spinicaudatan carapaces (up to 10 individuals per valve of 4 mm in length) or detached from their original substrate within the Changhsingian Bugarikta Formation. Three individuals were found on a bivalve shell in the Kedrovka Subformation (Fig. 3d).

Various attachment scar morphologies are observed in the form of substrate bioimmuration (Figs 3c, d, 4c, d). Linear depressions are visible at the basal surface of some detached tubes, which may have been formed due to microconchid attachment to firm elongated objects such as plant stems (Fig. 3c). In the Anakit-2 locality, dense detached flattened tube accumulations

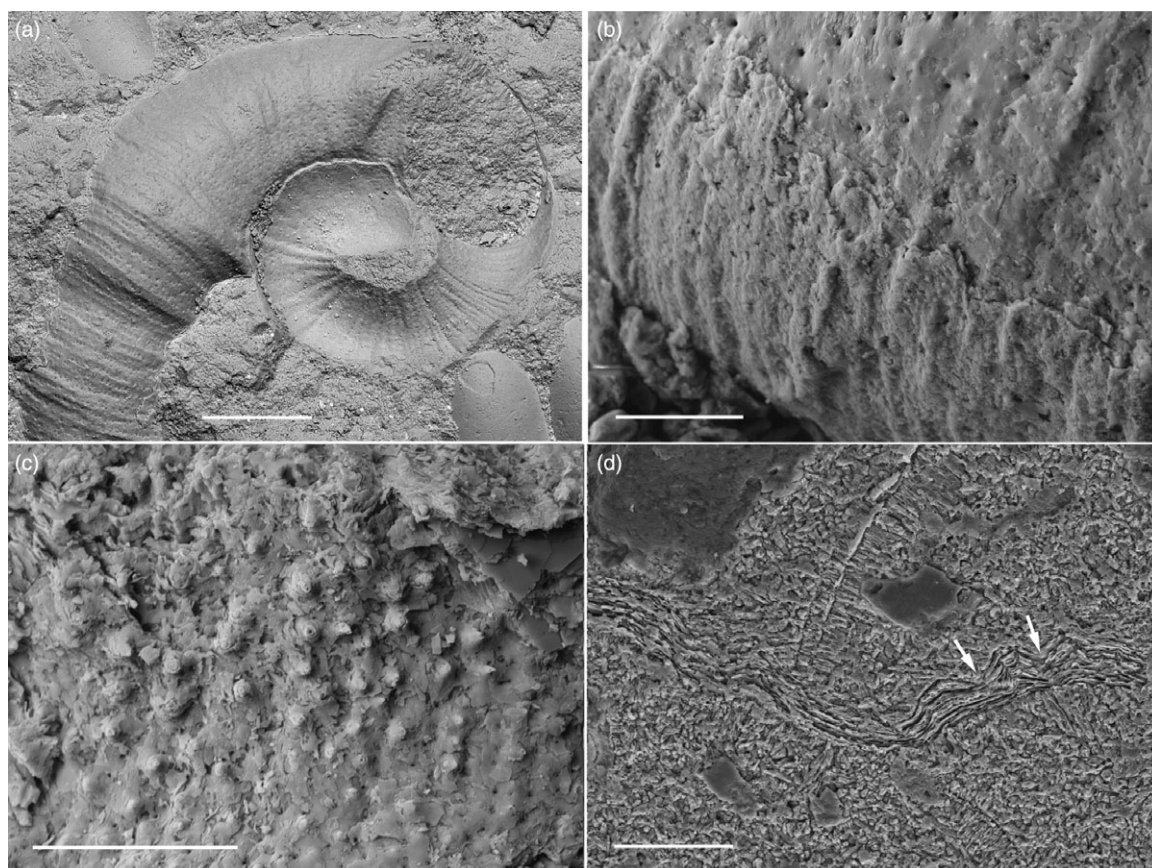


Fig. 5. Microconchid tube microsculpture and microstructure from the Bugarikta Formation, uppermost Permian (Changhsingian), Tunguska Basin, Krasnoyarsk region, Russia; ESEM. (a) PIN 2402/36a, shell showing bulbous embryonic chamber and imprint of inner surface microsculpture; tube is surrounded by several ostracod carapaces, Nizhnyaya Lyulyuikta section. (b) PIN 5381/349, lamellar tube and inner mould showing microsculpture and punctae, Anakit section. (c) PIN 2362/27, BSE, tube inner surface showing tuberculate microsculpture, Anakit section. (d) PIN 2402/36b, SE, section of lamellar tube wall with inflections pierced by canals (arrowed), Nizhnyaya Lyulyuikta section. Scale bars: (a) 0.2 mm and (b–d) 0.05 mm.

(over 60 individuals per 10 cm²) are found on the same bedding plane covered with a thin volcanic ash layer. EDS analysis indicates that the tubes have a low magnesium-calcite composition, except for those of Anakit-2 locality where EDS data yield oxygen and silicon with subordinate amounts of iron, aluminium, calcium, potassium and sulphur in proportions broadly similar to those present in the sedimentary matrix. At Anakit-2 the microconchid tubes are crushed and fractured, and elemental analysis reveals their replacement either by silica or by a K,Ca-silicate, most likely a clay mineral (Fig. 3b).

Tubes are generally small (0.1–1.6 mm in diameter) planispiral tightly coiled with rapidly increasing diameters, but some specimens display slight uncoiling in later growth stages (Figs 3c, 5a). Dextrally (clockwise) and sinistrally (anticlockwise) coiled tubes co-occur in the same aggregations of the similarly well-preserved shelly specimens, but dextral forms prevail. The embryonic chamber is bulbous, closed, up to 0.2 mm in diameter (Figs 3b, 4d, 5a). As the successive whorls overlap minimally, coiling is tight evolute showing older whorls in a broad and almost circular umbilicus. The umbilical width ranges from 0.3 to 0.4 mm, increasing slightly in larger individuals where it is not directly correlated with an increase in tube diameter. The umbilical edge is rounded and characterized by a relatively low-angle slope. Tubes reach their maximum height about the midline. The lower attachment surface of the tubes is flattened and their upper free surface is inflated (Fig. 4c, d). The aperture

is round to oval, up to 0.6 mm in diameter. Externally, the tubes are regularly ornamented by fine, poorly to moderately developed, transverse growth bands (Figs 3b, 4c, 5b). The bands are 11–12 µm wide and are spaced at regular intervals of the same width accentuated by transverse ribs, which do not cross the entire tube width. The outer surface is covered with evenly spaced tubercles (c. 1 µm in diameter), which are mostly arranged in transverse rows following the ribs, and with a faint wavy transverse striation (Figs 4c, d, 5b). The tube wall is microlamellar, foliated and is regularly traversed by pores 1–3 µm in diameter that are restricted to inter-rib depressions and are somewhat scarcer than the tubercles (Fig. 5b). The inner tube surface is covered with evenly spaced inward inflections of microlamellae-forming tubercles that are penetrated by radial canals (punctae) connecting the outer pores with the tube interior, and have somewhat smaller pits corresponding to the outer surface tubercles (outwardly pointed microlamellar inflections devoid of canals, i.e. pseudopunctae; Fig. 5a, c, d).

In general, these tube characteristics conform to the genus *Microconchus* Murchison, 1839 (family Microconchidae Zatoń & Olempska, 2017). However, the specimens of the Tunguska and Kuznertska basins differ in detail from all formally described Late Permian and Early Triassic microconchids, and likely belong to a new species that is unique among known microconchids in having both punctae and pseudopunctae (Fig. 5a, c, d).

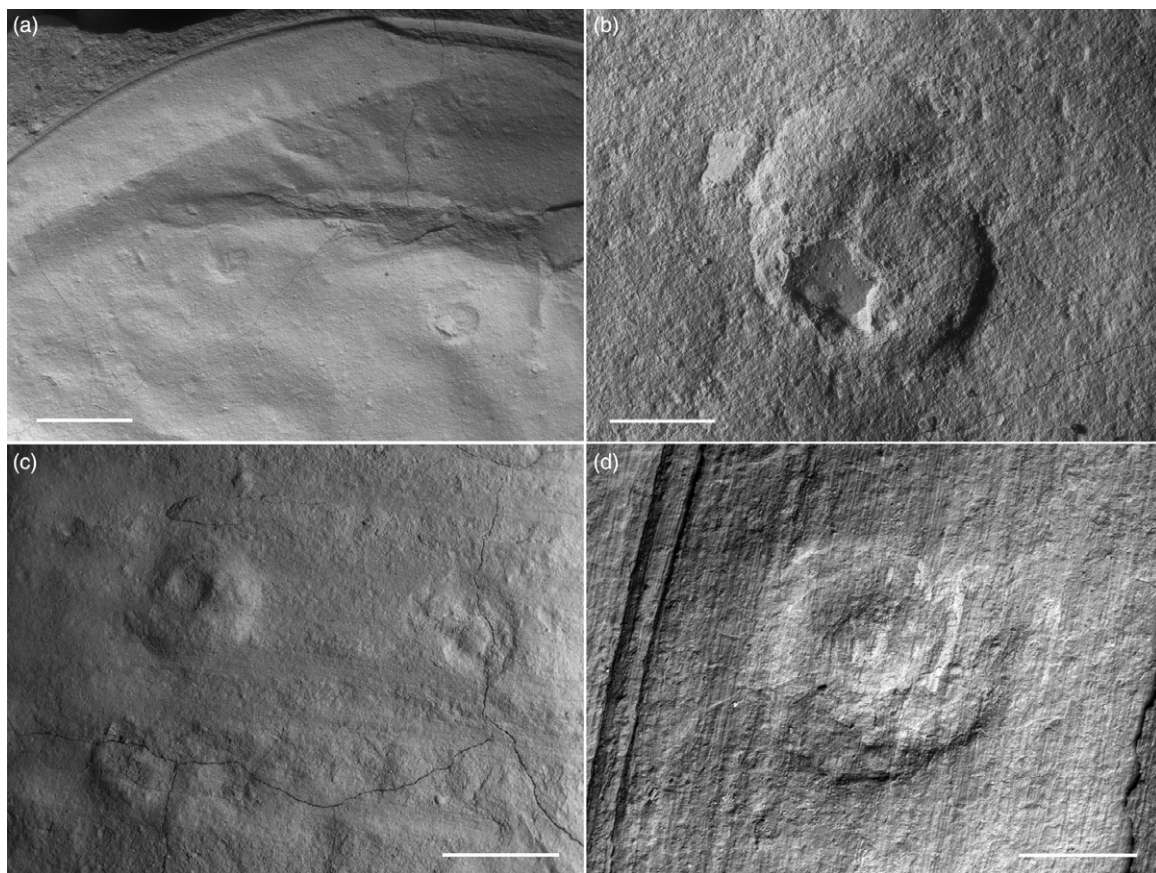


Fig. 6. Moulds of microconchid tubes from the Petropavlovka Formation, Lower Triassic (Olenekian), Petropavlovka III section, southern Cis-Urals, Orenburg region, Russia; ESEM (BSE). (a) PIN 5620/217, moulds on horseshoe crab head shield. (b) Detail of (a). (c) PIN 5640/218, moulds on plant stem with veins. (d) PIN 5640/213, SEM, detail of Figure 7a showing stem venation. Scale bars: (a, c) 2 mm; (b) 0.5 mm; and (d) 1 mm.

4.b. Early Triassic microconchids of Petropavlovka

In the Olenekian Petropavlovka Lagerstätte, complete or partially preserved ferruginous moulds of microconchid tubes are found on a horseshoe crab head shield (2) and aggregated on fragments of terrestrial plant stems (over 30), but not on the leaves. The moulds are accentuated by bright reddish accumulations of unspecified iron (oxyhydr)oxide minerals resulting from the oxidation of pyrite. SEM and EDS investigations show the crystal concentrations to consist of densely packed clusters of dodecahedral pyrite pseudomorphs ranging from 0.5 to 10.0 μm in size (Figs 6d, 7c, d).

The tubes are planispiral tightly coiled, small (0.5–2.5 mm in diameter) and with no tendency to uncoil in later growth stages (Figs 6b, 7b). Tube diameter increases continuously, resulting in a moderate overlapping of successive whorls. Tubes reach their maximum height about the umbilical edge, next to the midline. Dextrally and sinistrally coiled tubes co-occur in the same aggregations. The lower attachment tube surface is flattened and its upper free surface is convex. The tube umbilicus is open, circular and moderately wide in all specimens; the umbilical width ranges from 0.35 to 0.70 mm, slightly increasing in larger individuals. The umbilical edge is rounded and characterized by a relatively flattened low-angle slope. The umbilical width is not always correlated with an increase in tube diameter. The tube aperture is rounded to oval, and up to 0.7 mm in diameter.

Based on the planispiral coiling and open umbilicus, the specimens from the Petropavlovka Lagerstätte resemble to some extent the type species *Microconchus carbonarius* Murchison, 1839,

including the specimens from its Pennsylvanian (Carboniferous) population of Nova Scotia, Canada described by Zatoń *et al.* (2014a), and are tentatively assigned to the genus *Microconchus*. An almost invariable tube shape independently of dextral or sinistral coiling indicates that all the specimens probably belong to the same species, but unequivocal identification is not possible as neither skeletal carbonate nor surface ornamentation are detected. It is, nevertheless, possible that two approximately equally represented species with differently coiled tubes are present, similar to some other microconchid populations (Brönnimann & Zaninetti, 1972).

5. Discussion

5.a. Lacustrine microconchid associations of the Tunguska and Kuznetsk basins

5.a.1. Latest Permian continental environments and palaeocommunities of Siberia

Despite the relative remoteness of the Tunguska and Kuznetsk basins, these vast Siberian regions occur within the same northeastern Asian area of Pangea that witnessed one of the major LIP eruptions in the Earth's history, at the end Permian – Triassic transition (Fig. 1). All the Changhsingian sections of both basins were located far inland among volcanic landscapes, which hosted numerous lakes and rivers under dense mesic forests (Neustrueva & Bogomazov, 1987; Davies *et al.* 2010; Budnikov *et al.* 2020). The forests were dominated by ferns, peltasperms and conifers (Dobruskina, 1994; Mogutcheva, 1987, 2016; Sadovnikov, 2008;

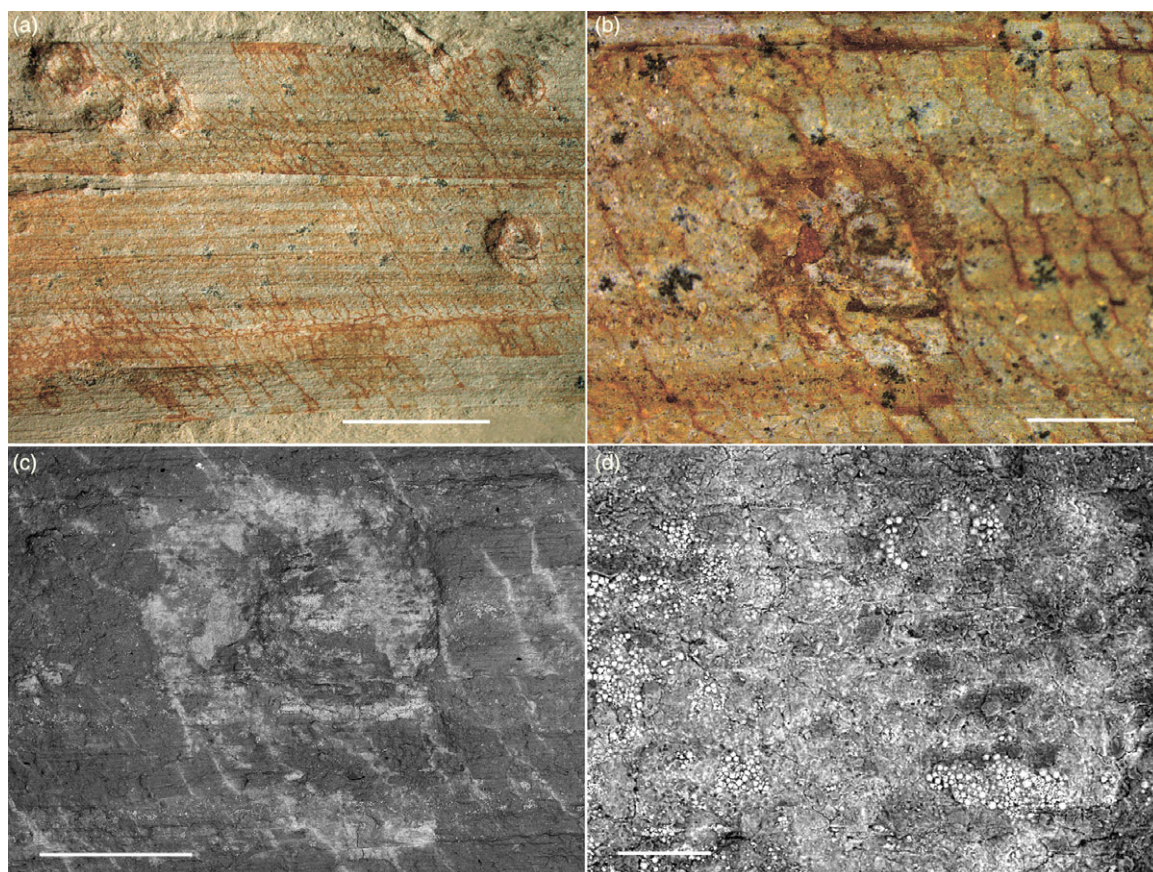


Fig. 7. (Colour online) Microconchid tubes encrusting plant stems from the Petropavlovka Formation, Lower Triassic (Olenekian), Petropavlovka III section, southern Cis-Urals, Orenburg region, Russia. (a) PIN 5640/213. (b) Detail of (a), diffuse light. (c, d) Details of (a) showing pyrite dodecahedron clusters replaced with iron (oxyhydr)oxides, ESEM (BSE). Scale bars: (a) 5 mm; (b, c) 1 mm; and (d) 0.1 mm.

Mogutcheva & Krugovykh, 2009; Karasev, 2015) and provided ecological niches for abundant and diverse insects. Over 600 fossil insect specimens were collected along the Nizhnyaya Tunguska River, comprising abundant and diverse beetles, grylloblattids, mayflies, scorpionflies, cockroaches, hemipterans, neuropterans and orthopterans; beetles belonging to eight different families and grylloblattids (four families) dominated here (Aristov, 2011; Aristov *et al.* 2013; Bashkuev, 2013; Sinitshenkova, 2013; Yan *et al.* 2018). Similarly, a rich insect fauna of beetles, grylloblattids, mayflies, cockroaches, hemipterans, neuropterans, orthopterans, stoneflies and webspinners is discovered in the Kedrovka Subformation of the Kuznetsk Basin at Babiy Kamen' (Shcherbakov, 2008c; Aristov *et al.* 2013; Ponomarenko & Volkov, 2013).

The lakes were populated by abundant and diverse charophytes, bivalves, gastropods, spinicaudatans and ostracods (Neuburg, 1936; Kukhtinov & Neustrueva, 1986; Sadovnikov & Orlova, 1995; Sadovnikov, 2008, 2016; Mogutcheva & Krugovykh, 2009; Davydov *et al.* 2019; Silantiev *et al.* 2020). In the Tunguska Basin, unequivocally aquatic insects were represented by mayfly nymphs *Khungtukunia sibirica* of the family Vogesonymphidae (Sinitshenkova, 2013) and by the earliest whirling beetle *Tunguskagyryrus planus* (Gyrinidae) featuring a smooth streamlined drop-shaped body with very specific completely divided compound eyes and paddle-shaped antennal pedicels (Yan *et al.* 2018). Aquatic insects of the Kuznetsk Basin are more diverse and include mayflies (of which only adults have been found), various beetles (Schizophoridae, Haliploidea, Hydrophilidae) that typically live in the water in all stages of their

life cycle, and presumably semiaquatic chaulioditid grylloblattids (Shcherbakov, 2008c; Ponomarenko & Volkov, 2013). For instance, the extinct family Schizophoridae was characterized by an elytra-thoracic interlock ('schiza') considered an amphibiotic adaptation (Shcherbakov, 2008b).

Increased alkalinity of the lakes is thought to be due to intense volcanic outgassing and evidenced by the development of a calcareous cement that consolidates shellbed lenses, montmorillonite seams and common zeolite pseudomorphs after shells and plant fragments (Neuburg, 1936; Neustrueva & Bogomazov, 1987). Specifically, the increased alkalinity could be due to the breakdown of volcanic ash glass particles reacting with lake pore water. The result was water supersaturation in silica (Calvert, 1974; Hethke *et al.* 2013; Fürsich & Pan, 2016), which facilitated dissolution of calcareous shells and their preservation as fine fabric replacive silica, as in the Anakit-2 locality that was especially rich in pyroclastic sediments (Fig. 3b). The same process could inhibit the proliferation of a rich aquatic insect fauna in the Tunguska Basin. Such a fauna, although present, is restricted to the few low-abundance species listed above. However, even this depauperate aquatic insect palaeocommunity required fresh- to slightly brackish water conditions (salt concentrations below 3–8‰) judging by the presence of mayfly larvae and aquatic beetles, which lack physiological mechanisms for proper osmoregulation (Chadwick *et al.* 2002; Bauerfeind, 2003). In turn, the abundance of filter feeders (microconchids, small bivalves) and fine-deposit feeders (ostracods, spinicaudatans and certain mayfly larvae) points to eutrophication of the water bodies.

Fishes of the Tunguska Basin comprised heavily armoured predator neopterygians *Tungusichthys acenrophoroides*, *Arctosomus sibiricus*, *Evenkia eunotoptera* and *Eoperleidus bergi*. These represent four families from orders affiliated with stem groups of relict freshwater gars in the orders Lepisosteiformes and Amiiiformes (Arratia, 2004), two of which were restricted to a few freshwater basins of northern Asia (Sytchevskaya, 1999). The only local amphibian *Tungusogyrinus bergi* was a small neotenic newt-like temnospondyl that was thought to have maintained external gill breathing during its entire life cycle, and possessed uncommon tricuspid dentition similar to that of anuran tadpoles, adapted to scrape algae; this is a feature typical of the latest representatives of branchiosaurids (Shishkin, 1998; Werneburg, 2009). Some elements of this rich fauna (certain spinicaudatan species and the newt-like amphibia) suggest the possibility that lotic conditions were present at least temporarily (Sadovnikov, 2008; Werneburg, 2009).

The overall abundance and diversity of the floras and faunas present in the Tunguska and Kuznetsk basins indicate that they were neither depauperate nor stressed, despite high levels of local volcanic activity, which resulted in ash fall 'killing' beds. In general, areas fertilized by nutrient-rich volcanic ashes were suitable for rapid plant growth during calm episodes, which in turn provided abundant food for rapidly reproducing insects. For instance, tree fern species, which comprised more than half of the diversity in the Tunguska Basin flora, proliferate and demonstrate high growth rates on volcanic substrates in Hawaii and New Zealand (e.g. Nicholls, 1959; Durand & Goldstein, 2001; Shepherd *et al.* 2007), while abundant bacterio- and phytoplankton blooms occur as a result of fertilization with volcanic ash leachate nutrients (Zhang *et al.* 2017). It is noteworthy that large vertebrates were not detected either in the Tunguska Basin, or in the coeval Kuznetsk Basin lakes, where the lacustrine vertebrate fauna was represented only by 10 to 300-mm-long individuals (Sytchevskaya, 1999; Shcherbakov *et al.* 2002; Werneburg, 2009). The abundance of endemics of a high taxonomic rank (fishes, amphibians) and progenitors of Mesozoic groups (plants, insects) is typical of rapidly evolving and changing volcanic landscapes, similar to the present Great Lakes of the East African Rift, which provide a wide test site for adaptive radiation and explosive speciation (Salzburger *et al.* 2014; Lyons *et al.* 2015).

5.a.2. Palaeoecology of the latest Permian microconchids of Siberia

Microconchids became part of this freshwater biota but were the only epibenthic encrusting filter feeders. They settled on spinicaudatan carapaces and bivalve shells and commonly formed aggregations of tubes of a wide size range densely covering this substrate (Figs 3a, 4a). Such an ecological strategy resulting in a specific encrusting morphology, which is probably plesiomorphic for microconchids, is commonly found on different hard substrates under many conditions (e.g. Sandberg, 1963; Kelber, 1987; Zatoń *et al.* 2013; Matsunaga & Tomescu, 2017). Dense settlements of microconchids representing the full local size range are present on small areas of the same substrate. There is no evidence of differentiation of growth conditions among microconchids of various sizes randomly distributed along the same substrate, which suggests coexistence of different generations of the same population rather than unequal growth rates among individuals of the same age. Several generations of these diminutive encrusters commonly grew in aggregations (e.g. Zatoń & Krawczyński, 2011; Caruso &

Tomescu, 2012; Zatoń & Peck, 2013). In the Nizhnyaya Tunguska microconchid populations, a settlement of older individuals likely facilitated further larval settlements because parental aggregations even by themselves provided hard substrates for attachment. Similar aggregative behaviour is ubiquitous for many extant encrusting invertebrates, such as the small polychaete tubeworm *Spirorbis* (Knight-Jones, 1951).

Based on the specific ornamentation consisting of concentric growth lines and fine wavy radial striation, it is possible to ascertain that the majority of spinicaudatan carapaces settled by microconchids are belonged to *Bipemphigus gennisi*. This species was among the largest spinicaudatans (over 5 mm long) and was probably a benthic deposit-feeding crustacean resting on the lateral surface of one valve at the water–sediment interface, similar to its extant relatives (Vannier *et al.* 2003). Due to a specific spinicaudatan exuviation with preservation of the old carapace outer layers, it cannot be ruled out that these microconchids settled on living animals but eventually sentenced the host to death by locking the valves. Such extremely dense and heavy microconchid aggregations consisting of large individuals were able to develop on empty carapaces accumulating at the bottom of the lakes (Figs 3a, 4a, 8). On a bivalve shell, encrusting microconchids were small and left scars featuring an irregular network formed by a partial dissolution of the host valve surface (Fig. 3d). Because freshwater bivalves are covered with thick periostraca (Harper *et al.* 1997), scars formed on a calcareous layer are indicative of a post-mortem settlement. Among the local fauna, the small branchiosaurid armed with tricuspid teeth adapted for scraping might have been a threat for these tiny encrusters (Fig. 8).

In the Nizhnyaya Lyulyuikta section, microconchid tubes formed shellbeds of a grainstone–packstone grade together with calcareous charophycean gyrogonites, small gastropod conchs, spinicaudatan and ostracod carapaces of the same size range. The presence of attachment scars on microconchid tubes indicates that they were encrusters when alive, as noted in other microconchids from the same localities when they are preserved in situ. Such microconchid tubes preserve linear groove-like attachment scars, the shape of which indicate that such individuals, when alive, have been settled on cylindrical plant stems or algal thalli (Fig. 3c, bottom left specimen).

5.b. Lacustrine Petropavlovka microconchid association

5.b.1. Early Triassic continental environments and palaeocommunities of the southern Cis-Urals

Sedimentological and palaeontological data indicate that the Petropavlovka Lagerstätte in the southern Cis-Urals was probably formed within an ephemeral pond on a vast floodplain. This allowed rapid colonization by opportunistic animals until the next dry season. This fauna was represented by ostracods and spinicaudatans with resting egg clutches, which could endure long periods of desiccations (Horne & Martens, 1988; Vannier *et al.* 2003), lungfish aestivating in burrows (Hasiotis *et al.* 1993), and microdrile clitellates forming cocoons that are very resistant to physical and chemical decay (Manum *et al.* 1991). These organisms are preserved in the Petropavlovka Formation either as body fossils – ostracods, spinicaudatans and a microdrile (Tverdokhlebov, 1967; Shcherbakov *et al.* 2019, 2020) – or, in the case of dipnoan fish, as both body and trace fossils (Minikh & Minikh, 1997; Sennikov, 2018). Common spinicaudatans and sparse horseshoe crabs of the Petropavlovka Lagerstätte also typified Mesozoic freshwater communities (Lamsdell, 2016; Hethke *et al.* 2019),

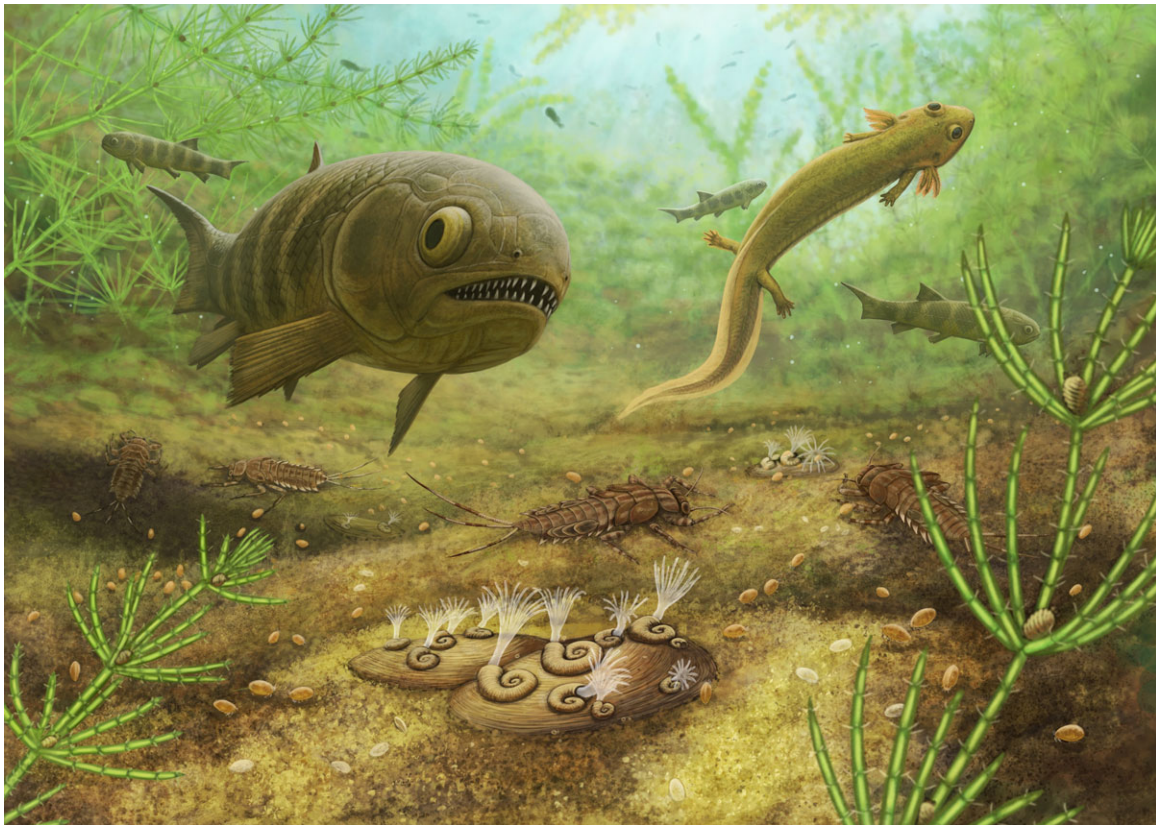


Fig. 8. (Colour online) Reconstruction of a latest Permian (Changhsingian) lacustrine community in the Tunguska Basin: neopterygian fishes *Tungusichthys acentrophoroides* and branchiosaurid amphibian *Tungussogyrinus bergi* in the water, mayfly larvae *Khungtukunia sibirica*, ostracods *Darwinula* and clam shrimp *Bipemphigus* carapaces encrusted by gregarious microconchids at the bottom among charophyceans (artwork: Andrey Atuchin).

while remains of diverse temnospondyl amphibians with specific adaptations for feeding on aquatic animals characterize the entire formation (Shishkin *et al.* 1995; Novikov, 2018; Sennikov & Novikov, 2018).

As a whole, this assemblage represents a common Early Triassic lacustrine fauna, while terrestrial arthropods, including insects and millipedes, and plants constitute a shore community inhabiting a floodplain environment (Kozur & Weems, 2010; Żyła *et al.* 2013; Kustatscher *et al.* 2014; Haig *et al.* 2015; Feng *et al.* 2018).

The presence of such a specific palaeocoenosis, in addition to the absence of evaporite minerals, suggests freshwater conditions for the formation of the Lagerstätte, even though most animal groups of the Petropavlovka ecosystem were able to survive and even disperse in brackish basins, such as microdriles (up to saline littoral areas; Brinkhurst, 1971), horseshoe crabs (up to normal marine; Lamsdell, 2016), ostracods (up to hypersaline conditions; De Deckker, 1983; Boomer *et al.* 2016) and spinicaudatans (up to 15 g L⁻¹ salinity level; Timms & Richter, 2002). Coeval lungfishes including *Ceratodus* (Clement & Long, 2010; Frederickson & Cifelli, 2017) and even rhytidosteid temnospondyls – a rare case for amphibians – were able to tolerate saline waters (Jones & Hillman, 1978; Novikov, 2018). The existence of at least temporal brackish conditions would be a plausible state of the Petropavlovka water body, but other amphibian remains (capitosaurids and brachyopoids) characterizing the formation have never been recorded in assemblages with marine fossils (Novikov, 2018). Finally, the overwhelming majority of the Permian and later dipnoans were restricted to freshwater (Kemp *et al.* 2017).

5.b.2. Palaeoecology of the Early Triassic microconchids of the southern Cis-Urals

Two microconchid tubes are attached to a single xiphosuran head shield, but it is impossible to establish if this was a living association, encrustation of an abandoned exuvium, or simply a dead body fragment (Fig. 6a, b). By contrast, aggregative microconchid associations on terrestrial plant fragments consisted of individuals representing different growth stages and restricted to plant stems (Figs 6c, d, 7). Such stems with dense parallel ridges probably represented a relatively firm substrate that was permanently submerged in a lake body and therefore permanently available for a colonization by encrusters (Figs 6c, d, 7a, b, 9). Petropavlovka microconchids belong to the category of planispiral tubes that are completely substrate-cemented. This habit was interpreted as an adaptation for achieving a firm tube attachment under conditions when only a limited hard substrate area was available (Vinn, 2010).

Commonly, microconchid tubes, attached to either plant fragments or animal shells accumulated under freshwater conditions, are poorly preserved (Zatoń & Mazurek, 2011; Caruso & Tomescu, 2012; Zatoń & Peck, 2013). The case of the Lower Devonian Beartooth Butte Formation (Wyoming, USA) is especially typical, as microconchid tubes were repeatedly attached to form aggregations on horizontal lycophyte stems when they were submerged during occasional flood events (Matsunaga & Tomescu, 2017). Similar preservation is observed in microconchids from the Petropavlovka Lagerstätte.

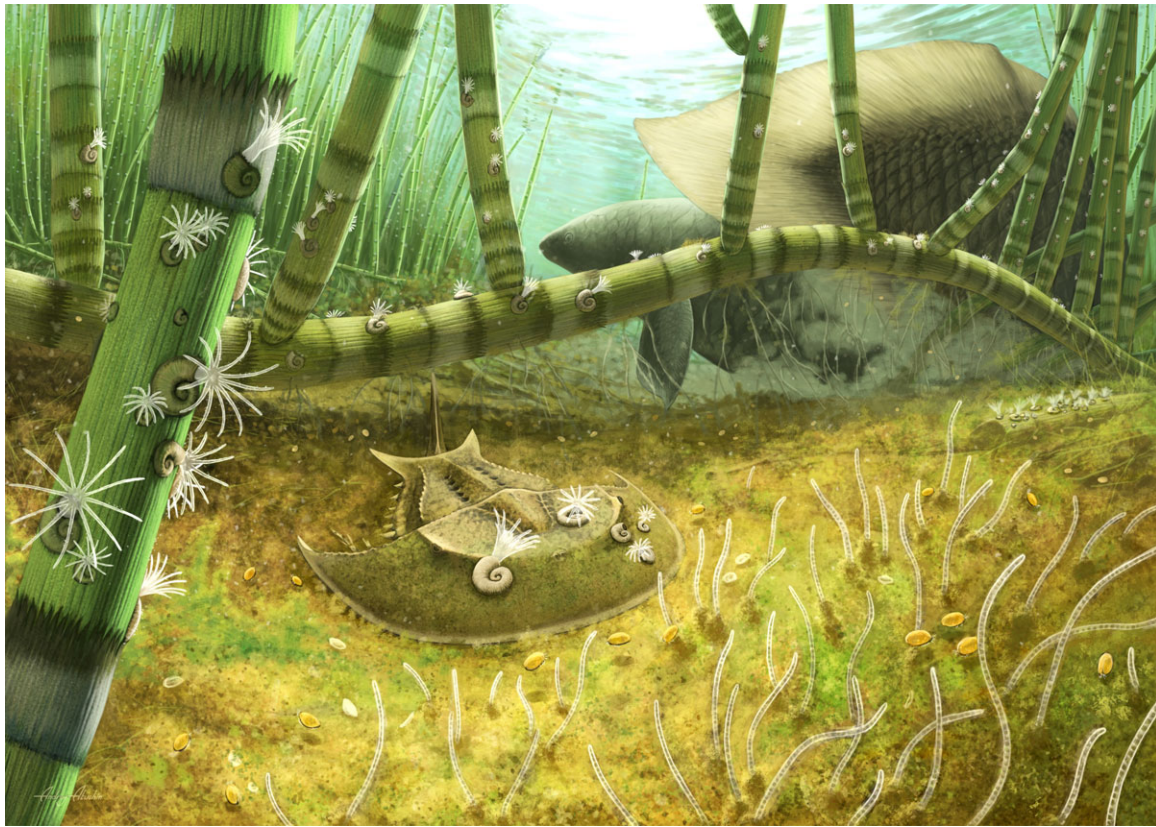


Fig. 9. (Colour online) Reconstruction of an Early Triassic (Olenekian) lacustrine community in the Cis-Urals: microconchid settlements on submerged sphenopsids and a horse-shoe crab, benthic ostracods and 'microdrille' clitellate settlement, the lungfish *Ceratodus* on the background (artwork: Andrey Atuchin).

Confirming that the water body that supported the Petropavlovka ecosystem was nutrient rich is problematic. We note that dense accumulations of primarily pyrite dodecahedra restricted to attached microconchid tubes, stem veins and rootlets, to which they impart a rusty tint, are common on bedding planes (Fig. 7b–d). As the availability of organic matter that can be metabolized by sulphate-reducing bacteria is one of principal factors of pyrite formation, a high carbon/sulphur ratio might be expected for the appearance of abundant pyrite clusters in a fresh-water basin (Berner, 1984; Hethke *et al.* 2013). In turn, the decomposition of organic matter by sulphate-reducing bacteria favoured low-pH conditions (increased acidity) and would lead to the dissolution of skeletal carbonate and precipitation of early diagenetic pyrite (Butts & Briggs, 2011; Fürsich & Pan, 2016). With the increased supersaturation of a monosulphide phase, the pyrite crystal habits change from cubic to pyritohedron and other complex crystals, while a wide size range (from 0.5 to 10.0 μm in diameter), including abundant crystals of larger sizes within dominantly dodecahedral pyrite populations, suggests continuous weakly oxygenated lake bottom conditions (Wang *et al.* 2013; Fürsich & Pan, 2016). This sedimentological feature might be indicative of abundant decaying plant and animal remains consumed by benthic bacterial associations at the lake bottom, but not for the redox state of the water column itself. However, a lacustrine palaeoecoenosis, consisting mostly of ceratodontids hiding in aestivation burrows, limulids and abundant microconchids that represent the major suspension feeders in the Petropavlovka ecosystem, points to a meromictic eutrophic lake.

5.c. The fresh- and brackish-water microconchid controversy

Fresh- to brackish-water occurrences of microconchids have been documented in the Lower Devonian – Upper Triassic strata (Taylor & Vinn, 2006; Caruso & Tomescu, 2012; Zatoń *et al.* 2012; Zatoń & Peck, 2013; Matsunaga & Tomescu, 2017). Subsequently, an autochthonous origin for microconchid occurrences in any fresh- and brackish-water continental palaeoenvironments unconnected to the ocean has been disputed by Gierlowski-Kordesch & Cassle (2015). These authors explained such occurrences as representing coastal environments, either within a non-marine–marine transition (tidal coast, estuary, delta) or on a distal transition floodplain within a low-gradient coastal area potentially affected by rare storm surges, tsunamis and sea-level oscillations. Indeed, the very presence of aggregative microconchid palaeocommunities in ancient fresh- and brackish-water sites has been questioned. Instead, preservation as single tubes strewn across bedding planes or randomly dispersed through the sedimentary matrix, with only temporary larval settlements on terrestrial plant remains, has been proposed, where larvae brought into restricted fresh- and brackish-water continental environments by sea surges did not mature (Gierlowski-Kordesch & Cassle, 2015, p. 216).

Zatoń *et al.* (2016b) criticized these interpretations, suggesting that the reductionist phoronid (extant lophophorate group) model, used by Gierlowski-Kordesch & Cassle (2015) to estimate microconchid salinity tolerance, had no support. Zatoń *et al.* (2016b) also pointed out that a number of localities, that lack even poorly

preserved marine shells transported by storm surges and tsunamis, contain microconchids including fully developed mature individuals associated only with remains of fresh- and brackish-water organisms, including charophyceans and specialized freshwater bivalves, spinicaudatans and ostracods.

The uppermost Permian and Lower Triassic localities described here indicate that microconchid populations were always aggregative, composed *in situ* of individuals of a wide age range, and were entirely restricted to firm substrates encrusting fresh or slightly brackish water horseshoe crabs, spinicaudatans, bivalves and submerged plant or algal organs. These localities were not unique for the Permian and Early–Middle Triassic periods. Palaeogeographic reconstructions indicate that microconchid occurrences associated with fresh- and brackish-water animals and plants are present in: the Lower Permian (Asselian) Altenglan Formation of the Saar Nahe Basin in Germany, where microconchids are associated with freshwater stromatolites (Stapf, 1971; Schäfer & Stapf, 1978; Schultze, 2009); the Asselian–Artinskian coal-bearing Upper Sadong Series in South Korea, where these microfossils encrusted land plants (Shikama & Hirano, 1969); the uppermost Permian (Changhsingian) floodplain Kul’chumovo Formation containing a rich assemblage of freshwater tetrapods, ostracods and bivalves in the southern Cis-Urals (Tverdokhlebov *et al.* 2005; Kukhtinov, 2017); and the Middle Triassic (Anisian–Ladinian) Ouled Chebbi Formation deposited within fresh- to brackish-water environments of Tunisia (Błazejowski *et al.* 2017).

In the Ladinian – lower Carnian lacustrine Madygen Lagerstätte of Kyrgyzstan, microconchid aggregations encrusting plant fragments are associated with charophyceans, aquatic liverworts (Ricciaceae), various freshwater bivalves, gastropods, phylactolaemate bryozoans (represented by flotoblasts), spinicaudatans, dipnoans, xenacanthid sharks and basal salamander-like urodeles, as well as several species of schizophorid beetles (Sikstel’, 1960; Ivakhnenko, 1978; Shcherbakov, 2008b; Moisan *et al.* 2012; Voigt *et al.* 2017; Schoch *et al.* 2020). The Madygen strata yield oxygen- and strontium-isotope records indicative of freshwater conditions, accumulated in an oxygenated perennial lake located several hundred kilometers away from the nearest marine shoreline within a warm temperate climatic zone (Voigt *et al.* 2017). Another conspicuous Middle Triassic (Anisian) deltaic–lacustrine Lagerstätte is the Grès à *Voltzia* in the Vosges, northern France, where faunas of a different provenance including a marine-influenced delta were discovered; again, microconchid aggregations are restricted to terrestrial plant fragments, bivalve shells and a fish (chondrichthyan?) egg capsule and associated only with limnomedusae, horseshoe crabs, euthycarcinoids, tadpole shrimps, spinicaudatans, abundant gilled mayfly and aquatic beetle larvae, aquatic insect egg clutches, lingulids and temnospondyl amphibians. This fauna characterizes the fresh- to brackish waters of a deltaic environment with ephemeral temporary channels and ponds (Gall, 1971; Gall & Grauvogel-Stamm, 2005; Sinitshenkova *et al.* 2005; Ponomarenko & Prokin, 2013). No transported and reworked microconchid tubes of marine origin are observed in other Lower and Middle Triassic probable lacustrine strata, including the Bromsgrave Sandstone Formation of England (Ball, 1980) and the Lower Keuper of southern Germany (Kelber, 1987; Kietzke, 1989). There the tiny tubeworms always encrusted terrestrial plant fragments, forming dense aggregations of multiple generations. Their settlements preserved in the Lower Keuper are especially remarkable, as microconchids varying in size from

0.35 to 2.25 mm were densely (over 50 individuals per 1 cm²) attached to submerged plant rhizomes (Kelber, 1987).

In summary, Permian and Early–Middle Triassic microconchids constituted an integral part of fresh- and brackish-water lacustrine ecosystems, where they formed dense, encrusting settlements on various firm substrates provided by terrestrial and mostly aquatic plants and animals. No reworked microconchid accumulations or scattered tubes, which could be interpreted as allochthonous remains transported from marine basins, have ever been detected in Permian and Triassic lacustrine strata.

5.d. Microconchids as disaster species

The concept of disaster forms was introduced by Schubert & Bottjer (1992) for opportunistic generalists, which were the taxa increased dramatically in range and abundance after severe mass extinctions, briefly proliferated during the time of biotic crisis invading vacant ecospace until forced out through competition with specialist taxa, and returned to low level of abundance afterwards. Since that time, this concept was widely used for a number of the earliest Triassic species and palaeocommunities (e.g. Hallam & Wignall, 1997; Kershaw *et al.* 2012; Benton & Newell, 2014; Song *et al.* 2016).

Microconchids were opportunistic generalists, and colonized any suitable, firm and hard substrate in a given environment (Fraiser, 2011; He *et al.* 2012; Zatoń *et al.* 2012, 2013; Zatoń & Peck, 2013; Taylor, 2016). The multiple dense microconchid tube accumulations interlaid with ash beds in the Tunguska Basin indicate that these animals were able to reproduce quickly. Freshwater basins of the Tunguska and Kuznetsk basin were particularly stressful environments undergoing extremely high temperature and redox oscillations during the Permian–Triassic transition.

These tiny encrusters often benefitted from a rich food supply, weak competition from other fouling animals and low predator pressure. Such favourable conditions would have typified, for instance, the Early Triassic Petropavlovka ecosystem. No other encrusters, not even single specimens, were established there. As tiny shelly lophophorates firmly attached to a substrate (where aggregating plants and flexed carapace fragments may also have provided some protection), they were not attractive prey for potential predators of Petropavlovka. These would have included horseshoe crabs, lungfishes and rhytidosteid amphibians. Rhytidosteids probably hunted armoured crustaceans (Sennikov & Novikov, 2018), dipnoans preyed upon various invertebrates, including large shelled individuals (Bemis & Lauder, 1986), and limulids fed on larger and “meatier” benthic animals (Błazejowski *et al.* 2017).

Moreover, the microconchids were among a tiny handful of marine organisms that survived the Permian–Triassic mass extinction and rapidly spread globally, despite the unstable conditions created by the eruption of the Siberian Traps that probably brought about sulphur pollution, ozone shield deterioration, ocean acidification, oxygen content lowering and enormous coal combustions contributing to severe greenhouse effect and carbon cycle destabilization (Retallack *et al.* 1996; Hallam & Wignall, 1997; Erwin, 2006; Knoll *et al.* 2007; Algeo & Twitchett, 2010; Kershaw *et al.* 2012; Payne & Clapham, 2012; Sun *et al.* 2012; Benton & Newell, 2014; Lau *et al.* 2016; van de Schootbrugge & Wignall, 2016; Benca *et al.* 2018; Wood & Erwin, 2018; Elkins-Tanton *et al.* 2020). In addition to diverse lacustrine environments varying from freshwater to harsh hypersaline basins during Early and early Middle Triassic time, microconchids globally occupied a wide

Table 2. Permian and Lower–Middle Triassic microconchid palaeogeographical and palaeoenvironmental occurrences

Locality number	Age and location	Patterns of occurrence	Palaeoenvironment	References
1	Early Permian, Artinskian–Kungurian; Arcturus Formation; Nevada, Utah, USA	Locally abundant	Inner carbonate shelf, coastal and restricted marine	Stevens (1966); Yancey & Stevens (1981)
2	Middle Permian; Whitehorse Formation; Kansas, Oklahoma, USA	Attached to bivalve shells	Coastal and restricted marine	Newell (1940); West <i>et al.</i> (2010)
3	Early Permian, Artinskian–Kungurian; Blaine and Dog Creek formations; Kansas, Oklahoma, Texas, USA	Present	Coastal and restricted marine, brackish water and dominantly continental	Clifton (1942); West <i>et al.</i> (2010)
4	Early Permian, Artinskian–Kungurian; Elm Creek, Valera, Bead Mountain and Leuders formations (Wichita–Albany Group); Texas, USA	Budding individuals, forming patch reefs	Shallow-marine subtidal under fluctuating salinity	Wilson <i>et al.</i> (2011)
5	Early Permian, Asselian; Laborcita Formation; New Mexico, USA	Encrusted stromatolites	Alluvial-plane to nearshore marginal marine conditions	Toomey & Cys (1977)
6	Early Permian, Artinskian; Hueco Group; New Mexico, USA	Detached in grainstone	Open normal marine to restricted platform interior and shelf	Toomey (1976); Lucas <i>et al.</i> (2015)
7	Middle Permian; Ford and Raisby formations; England	Attached to brachiopod shells and bryozoans	Marine	Götz (1931); Smith (1994)
8	Early Permian, Asselian; Altenglan Formation; Germany	Associated with stromatolites	Lacustrine	Stapf (1971); Schäfer & Stapf, (1978); Schultze (2009)
9	Late Permian, Changhsingian, Kul’chumovo Formation; southern Cis-Urals, Russia	Present	Seasonal temporary flows and ephemeral lakes on floodplain	Tverdokhlebov <i>et al.</i> (2005); Kukhtinov (2017)
10	Late Permian, Changhsingian; Bugarikta Formation; Tunguska Basin, Russia	Attached to spinicaudatan carapaces, forming grainstone-packstone	Freshwater lacustrine and lotic	This study
11	Late Permian, Changhsingian; Mal’tsevo Formation; Kuznetsk Basin, Russia	Attached to bivalve shell	Freshwater lacustrine	This study
12	Late Permian, Changhsingian; Bulla Member (Bellerophon Formation); Italy	Present	Shallow marine	Farabegoli <i>et al.</i> (2007)
13	Late Permian; Kirchaou; Tunisia	Present	Marine	Glantzboeckel & Rabaté (1964); Brönnimann & Zaninetti (1972)
14	Late Permian, Wuchiapingian; Episkopi Formation; Hydra Island, Greece	Aggregative	Outer shelf, above and below storm wave base	Shen & Clapham (2009)
15	Early Permian, Artinskian; Gharif Formation; Oman	Present	Fluvial to coastal plain and shallow marine	Schultze <i>et al.</i> (2008)
16	Late Permian, Changhsingian – Early Triassic, Induan; Heshan Formation; Guangxi-Zhuang, China	Attached to thrombolites	Isolated marine carbonate platform under oxygen-poor conditions	Yang <i>et al.</i> (2015a)
17	Late Permian, Changhsingian – Early Triassic, Induan; Daye Formation; Hunan, China	Attached to thrombolites-stromatolites and bivalve shells; forming grainstone-packstone	Isolated shallow carbonate platform and deeper outer shelf	He <i>et al.</i> (2012); Yang <i>et al.</i> (2015b); Foster <i>et al.</i> (2018)
18	Late Permian, Changhsingian – Early Triassic, Induan; Changxing Formation and Zaixia microbialites; Sichuan and Hubei, China	Clustered in thrombolites	Shallow-marine carbonate platform	Reinhardt (1988); Adachi <i>et al.</i> (2017)
19	Early Permian, Asselian to Artinskian; Upper Sadong Series; South Korea	Encrusted land plants	Fresh to brackish water	Shikama & Hirano (1969)
20	Early Triassic, Induan–Olenekian; Utah and Nevada, USA	Associated with sponges	Shallow-marine reefs	Brayard <i>et al.</i> (2011)
21	Early Triassic, Induan–Olenekian; Dinwoody, Virgin, Moenkopi and Thaynes formations; Montana, Wyoming, Idaho and Utah, USA	Attached to bryozoans and mostly to bivalves forming bioherms	Marine supratidal environments, upper shoreface to offshore carbonate ramp	Nützel & Schulbert (2005); Pruss <i>et al.</i> (2007); McGowan <i>et al.</i> (2009); Fraiser (2011); Zatoň <i>et al.</i> (2013)

(Continued)

Table 2. (Continued)

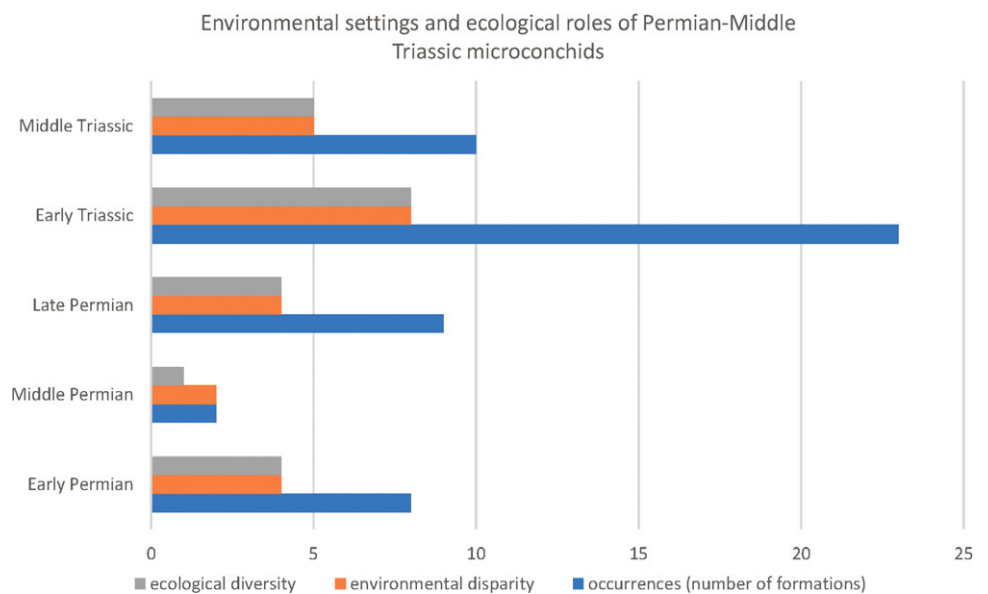
Locality number	Age and location	Patterns of occurrence	Palaeoenvironment	References
22	Early Triassic, Induan–Olenekian; Blind Fiord Formation; Ellesmere Island, Canada	Attached to bryozoans	Boreal marine carbonates	Nakrem & Ernst (2008)
23	Early Triassic, Induan; Wordie Creek Formation; East Greenland	Attached to bivalve shells and reef-building	Boreal shoreface and tidally influenced paralic settings	McGowan <i>et al.</i> (2009); Zatoń <i>et al.</i> (2016a, 2018)
24	Middle Triassic, Anisian; Bromsgrove Sandstone Formation, England	Encrusted, terrestrial plant leaves and stems	Freshwater, in channels, pools or lakes on flood plain	Ball (1980)
25	Middle Triassic; northern France	Encrusted cephalopod shells	Marine	Vossmerbäumer (1972)
26	Middle Triassic, Anisian; Grès à Voltzia; Vosges, France	Encrusted terrestrial plant leaves, bivalve shells and fish eggs	Tidal flats, brackish ponds and saltmarshes on deltaic plain	Gall (1971); Gall & Grauvogel-Stamm (2005)
27	Middle Triassic, Anisian–Ladinian; Trochitenkalk, Meißner, Freudenstadt, Karlstadt and Diemel formations, Muschelkalk; southern Germany	Encrusted bivalve, nautiloid and ammonite shells	Shallow to deeper ramp	Hagdorn (2010); Vinn (2010); Zatoń <i>et al.</i> (2013)
28	Middle Triassic, Ladinian; Lower Keuper; southern Germany	Attached to terrestrial plant lives and rhizomes; small aggregational mounds	Terrestrial to lacustrine; hypersaline to brackish water	Kelber (1987); Kietzke (1989); Hagdorn (2010)
29	Early Triassic; Bunter Series; western Poland	Microconchid–stromatolite build-ups	Shallow to marginal marine, upper subtidal – lower peritidal, sporadically in upper peritidal	Peryt (1974); Zatoń <i>et al.</i> (2012)
30	Early Triassic, Induan–Olenekian; Werfen Formation; South Alps, Austria and Italy	Encrusted microbialites and mollusc shells, grainstone	Tidal hypersaline to subtidal euhaline shallow carbonate platform	Brönnimann & Zaninetti (1972); Boeckelmann (1991); Posenato (2009)
31	Early Triassic, Induan; Svileuva Formation; Serbia	Present	Shallow carbonate platform	Sudar <i>et al.</i> (2018)
32	Early Triassic, Induan–Olenekian; Bódvaszilás Sandstone Formation; Hungary	Encrusted bivalve shells	Tidal-subtidal inner ramp under seasonal hypoxia and salinity fluctuations	Foster <i>et al.</i> (2015)
33	Early–Middle Triassic; Spain	Encrusted; rock forming detached	Shallow marine	Brönnimann & Zaninetti (1972)
34	Middle Triassic, Anisian to Ladinian; Ouled Chebbi Formation; Tunisia	Present	Fresh to brackish-water playa	Błażejowski <i>et al.</i> (2017)
35	Early Triassic, Induan; Kokarkuyu Formation; Turkey	Encrusted thrombolites	Shallow marine, episodically hypersaline	Heindel <i>et al.</i> (2018)
36	Early Triassic, Induan; Armenia	Associated with sponge-microbial reefs	Marine	Friesenbichler <i>et al.</i> (2018)
37	Early Triassic, Induan; Kangan Formation; central Iran	Encrusted thrombolites	Shallow marine, episodically hypersaline	Heindel <i>et al.</i> (2018)
38	Early–Middle Triassic, Induan–Anisian; Kangan Formation; Persian Gulf, Iran	In microbialites	Marine	Abdolmaleki & Tavakoli (2016); Mazaheri Johari & Ghasemi-Nejad, 2017
39	Early Triassic, Induan; olistostromes; Oman	Associated with crinoidal packstone	Marine neritic	Baud <i>et al.</i> (2015)
40	Early Triassic; Khuff Formation; central Saudi Arabia	Present	Marine tidal–intertidal	Vachard <i>et al.</i> (2005); Vaslet <i>et al.</i> (2005)
41	Early Triassic, Olenekian; Kockatea Shale; Western Australia	Present	Variable marginal shallow-marine to brackish eutrophic estuarine-like conditions	Haig <i>et al.</i> (2015)
42	Early Triassic, Olenekian; Petropavlovka Formation; southern Cis-Urals, Russia	Attached to horseshoe crab head shields and terrestrial plant stems	Lacustrine	This study
43	Middle–Late Triassic; Madygen Formation; Kyrgyzstan	Attached to terrestrial plants	Lacustrine	Voigt <i>et al.</i> (2017)

(Continued)

Table 2. (Continued)

Locality number	Age and location	Patterns of occurrence	Palaeoenvironment	References
44	Early Triassic, Induan; Luolou Formation; Guangxi-Zhuang, China and Vietnam	Cavity-dwellers in thrombolites	Shallow marine	Bagherpour <i>et al.</i> (2017)
45	Middle Triassic, Anisian; Qingyan Formation; Guizhou, China	Attached to shells	Shallow marine	Stiller (2000)
46	Early Triassic, Induan; Feixiangguang Formation; Sichuan, China	Attached to bivalve shells	Upper-slope seafloor under suboxic conditions	Godbold <i>et al.</i> (2018)
47	Early Triassic, Induan; Daye Formation; Zhejiang, China	In thrombolites	Shallow-marine carbonate platform under fluctuating redox conditions	Huang <i>et al.</i> (2019)
48	Early Triassic, Induan; Xiahuancang Formation; Qinghai, China	Encrusted bivalve shells	Marine lower shoreface bivalve–microbial mat-ground	Feng <i>et al.</i> (2019)
49	Early Triassic, Induan; Kamura Formation; Japan	In microbialites	Shallow-marine subtidal to intertidal	Sano & Nakashima (1997)

Fig. 10. (Colour online) Number of occurrences, environmental disparity and ecological diversity of microconchids during Early Permian – Middle Triassic epochs (Table 2). Number of occurrences is equalized with the number of formations yielding microconchids. Environmental disparity is recorded by a number of settings (up to 8) through an environmental profile (freshwater basins, hypersaline basins, marine supratidal, reefs, shallow subtidal, deep subtidal oxic, deep subtidal dysoxic/anoxic); boreal localities are ranked at additional score. The ecological diversity is demonstrated by eight different ecological roles associated with microbialites, sponge reefs, reef-forming, cavity-dwelling and rock-forming detached, and encrusting marine shelly fauna, fresh- to brackish-water shelly fauna and land plants.



range of marine zones from onshore, tidal to supratidal, shallow waters to a deeper outer shelf under oscillating redox conditions, on both carbonate and siliciclastic substrates. In general, twice as many microconchid occurrences are reported from the Lower Triassic than in the Upper Permian strata (Fig. 10, Table 2).

They became ubiquitous members of microbial (thrombolitic and stromatolitic), non-rigid spongal and bivalve reef-building communities (in places, even forming thickets on their own), filling the so-called Early Triassic ‘reef gap’, around the margins of all the main oceanic basins of the time, namely the Panthalassa, the Palaeo- and Neotethys, and the Boreal Ocean. They therefore inhabited different climatic zones from near the equatorial belt to moderately high latitudes (Peryt, 1974; Sano & Nakashima, 1997; Pruss *et al.* 2007; Nakrem & Ernst, 2008; Hagdorn, 2010; Brayard *et al.* 2011; He *et al.* 2012; Foster *et al.* 2015, 2018; Yang *et al.* 2015a; Zatoń *et al.* 2016a; Adachi *et al.* 2017; Godbold *et al.* 2018; Huang *et al.* 2019; Figs 1, 10; Table 2). In the Tethyan Realm, microconchids became so common that even a stratigraphic unit, named the *Spirorbis phlyctaena* (in fact, *Microconchus phlyctaena*; Vinn, 2010) Range Zone was established in the Lower Triassic Series, allowing for correlation of marine strata (Brönnimann & Zaninetti, 1972; Vaslet *et al.* 2005;

Mazaheri Johari & Ghasemi-Nejad, 2017). Some marine reef-building microconchids were able to withstand episodic hypersaline and ferruginous anoxic conditions, as suggested for the Neotethys (Heindel *et al.* 2018; Wood & Erwin, 2018). Aside from exceptional cases, when microconchids formed shelly packstone to grainstone (Baud *et al.* 2015; Yang *et al.* 2015b), these tiny creatures always encrusted firm substrates. In some localities, they colonized up to 50% of Early Triassic shelly animals, showing preference for the valves of the pterinopectinid bivalve *Claraia* (Fraiser, 2011), which was another common opportunistic survivor of the Permian–Triassic mass extinction (Ros-Franch *et al.* 2014; Table 2). In these instances, the density of microconchid encrusting populations reached 30–50 and up to 80 individuals per 1 cm² (Kelber, 1987; Zatoń *et al.* 2013, 2014b, 2016a), while in microbial reefs they comprised up to 3–5% of the framework, a sufficiently high figure for reef-builders (He *et al.* 2012; Heindel *et al.* 2018). Even biostromes (small, 3.5 cm thick and 30 cm in diameter) were built by interlocked microconchid individuals in the Early Triassic Series of East Greenland on their own (Zatoń *et al.* 2018).

The rapid appearance and disappearance of ephemeral continental basins as a result of fluctuating sea levels and the

beginning of the rifting of Pangaea, as well as an increase in runoff and evaporation (Labat *et al.* 2004) as a result of global warming, would have resulted in greater salinity fluctuations in shallow-water environments that would increase osmoregulation stress (Verschuren *et al.* 2000) and could have produced favourable conditions for the rapid expansion of opportunistic animals such as microconchids. Being resistant to salinity fluctuations, as well as (probably) to redox and temperature fluctuations, these small, lightly calcified tubeworm lophophorates became disaster stress-tolerators at the beginning of a new planetary era.

6. Conclusions

The uppermost Permian and lower Triassic lacustrine strata of the Tunguska and Kuznetsk basins, as well as those of the southern Cis-Urals in Russia, yield rich aquatic faunas, among which tubeworm microconchids were ubiquitous and one of the most abundant groups.

The latest Permian lacustrine faunas of the Tunguska and Kuznetsk basins existed during the initial phase of the Siberian LIP eruptions.

Despite an overall external similarity to tubeworm annelids, microconchids differ significantly from them in their tube microstructure and microsculpture that includes both punctae and pseudopunctae, and which they share with the lophophorates. Microconchids were the main component of the filter-feeding encrusting ecological guild in latest Permian and Early–Middle Triassic freshwater habitats, confirming earlier suggestions regarding their opportunistic nature (Fraiser, 2011; Zatoń *et al.* 2012, 2013).

During the Early and Middle Triassic epochs, in addition to lacustrine environments varying from fresh and brackish waters to hypersaline basins, microconchids occupied a wide range of marine zones from onshore shallow waters to a deeper outer shelf under oscillating redox conditions, on both carbonate and siliclastic substrates, and dispersed within different climatic zones from near the equatorial belt to moderately high latitudes.

We infer that microconchids capitalized on the habitat offered by Early and Middle Triassic lakes, where both the competition for substrates and predation pressure were very low in the aftermath of the severe Permian–Triassic extinction event that eliminated heavy calcifiers and grazers.

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