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Early acanthodians from the Lower Silurian of Asia

Valentina Karatajute-Talimaa and Moya Meredith Smith

ABSTRACT: Abundant microvertebrate remains from the Siberian Platform are described as early acanthodians. All are preserved with both excellent morphology and histology. They are assigned to a new order, Tchunacanthida, with two new families, Lenacanthidae and Tchunacanthidae. These comprise two new genera, *Lenacanthus* and *Tchunacanthus* with type species *L. priscus* sp. nov. and *T. obruchevi* sp. nov. The evidence from the morphology and histology is that they are the most ancient acanthodian scales so far found. The total collection of vertebrate material from the Irkutsk amphitheatre is described, together with their geological distribution, geographical range and systematic palaeontology. Head scales, tesserae of three morphotypes, transitional scales and body scales have been found. All comprise morphological sets as determined by comparison of morphology using SEM and of histology using Nomarsky interference optics. Observations of growth were possible from details of concentric lines on the crown and also from incremental layers seen in both horizontal and vertical sections. Starting from the primordial scale, consecutive layers are added, coronally, laterally, and deep in the corium onto the base; these occurred simultaneously in both crown and base. A type of areal-superpositional growth occurred in some body scales but in other scales there was little superpositional growth. It is concluded that *Tchunacanthus* possessed very solid body armour with tightly joined scales covering a large area of the body, and scale bases deeply set in the corium. Both tissues of the scales, dentine and bone, feature enclosed cells. This character is regarded as primitive within acanthodians, as in derived forms both tissues are acellular. Acanthodian scales are one of many examples of transformation from cellular to acellular tissue in evolution.

KEY WORDS: cellular hard tissue, mesodentine, scale growth, scale morphology, Siberian microvertebrates, Silurian fish

Ordovician and Lower Silurian (Llandoverian) vertebrates are seldom found in any of the fossiliferous rocks throughout the world. This phenomenon is due to a predominance of marine environments during the early Palaeozoic and unfavourable conditions for preservation of vertebrate remains on the sea bottom (Obruchev 1971). In addition, the exoskeleton of the most ancient vertebrates was formed of discrete scales, tesserae and/or individual dermal denticles, which very quickly disintegrated and dispersed after the death of the animal. One further reason for the rarity of vertebrate remains in the early Palaeozoic is the comparatively small probability of preservation of nearshore marine deposits (Obruchev 1971).

Investigation of vertebrate distribution in Silurian sections has shown the prevalence of their remains in deposits of the shallower facies of marine palaeobasins (Märss & Einasto 1978; Karatajute-Talimaa & Predtechenskyj 1995, fig. 2). This indicates that the search for microremains of early Silurian age should be undertaken in nearshore deltaic-lagoonal zones of epicontinental basins.

The description of a new order, two new families and two new genera and species of acanthodians from the Lower Silurian (Llandoverian) deposits of the Siberian Platform, Tuva and NW Mongolia are contained within the taxonomic account. The main material originates from the Irkutsk and Niuya-Beriosovo subregions, while the collections from the western district of the Pri-Yenisei subregion (Turukhansk and Tunguska districts) are less representative and could not always be defined to species. Data on acanthodians from the Upper Llandovery of NW Mongolia are included in the description of the genus *Tchunacanthus* gen. nov.

This material is stored in the Institute of Geology in Vilnius (Lithuania), collection numbers LIG 10 (Siberia and South Yakutia), LIG M-A (Mongolia) and LIG T-A (Tuva).

1. Historical account

The first report of Lower Silurian vertebrates from the Irkutsk amphitheatre (southern part of Krasnoyarsk district, Irkutsk District) was by Obruchev (1958); on the basis of very few scales they were determined as *Gomphonchus* sp. In the second half of the 1950s, Obruchev was given two further small collections of vertebrate microremains. The first was collected by Andrejeva in 1955 on the banks of the Tchuksha River. Later, Grebennikov and Smolianec collected a more representative sample of microremains from the head waters of the Parenda River (left tributary of the Tchuna River); these deposits had been attributed to the Bratsk Formation (uppermost Ordovician to lowermost Silurian). Now this part of the sequence is attributed to the Balturino Formation (Lower Silurian, Llandovery).

This description of acanthodian scales represents the evidence for the most ancient acanthodians ever found in the territory of Siberia and is the basis of this report. The total collection of material of Silurian vertebrates from the Irkutsk amphitheatre is reported here; the collection of Professor Obruchev was transferred to Dr Karatajute-Talimaa and later added to by that of Dr Moskalenko. Vertebrate samples were discovered at several levels (interval of depth from 32·1 m to 85·3 m) in Upper Llandovery deposits of borehole B-11 in the

Bratsk district (110 km N of Sedanovo settlement on the Bratsk–Ust–Ilimsk road; see Fig. 1). This small collection contains thelodont scales of *Loganellia sibirica* (Kar.-Tal.), the chondrichthyan *Elegestolepis conica* Kar.-Tal., and scales of acanthodians *Tchunacanthus obruchevi* gen. et sp. nov., described below, as well as *Tchunacanthus* sp. indet., Acanthodii indet., and many small spheres (well-rounded acanthodian scales). The best preservation of scales was found at a depth of 85·3 m in an interlayer of 20–30 cm in thickness, of red argillite with a bed of sandstone (Kanygin *et al.* 1984, fig. 11).

This material of Upper Ordovician (?)–Lower Silurian vertebrates from the Irkutsk amphitheatre was collected before the summer of 1982, when investigation of key and intermediate Silurian sections was organised in this region. This was conducted by lithologists and palaeontologists from the All Union Geological Institute (Leningrad), the Institute of

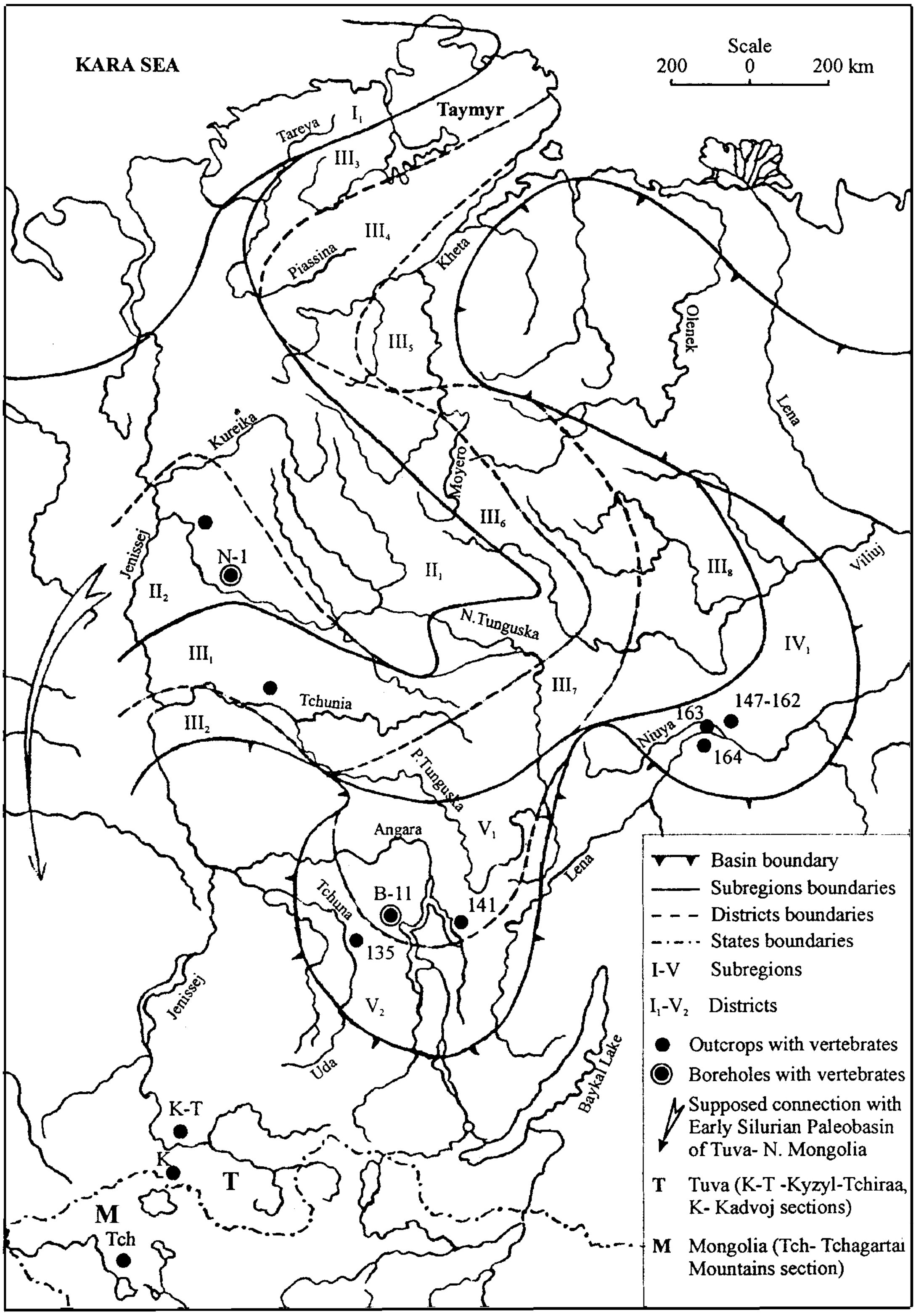

Figure 1 Stratigraphical zonation of the E Siberian Silurian palaeobasin and geographical position of the sections (after Karatajute-Talimaa & Predtechenskyj 1995, fig. 1; Tesakov 1999).

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Geology and Geophysics of the Siberian Branch of the Academy of Sciences of the USSR (Novosibirsk) and the Lithuanian Scientific Geological Research Institute (Vilnius). Palaeoichthyologists worked for three field seasons investigating ecostratigraphy of Silurian deposits on the Siberian platform. In 1982 the Silurian sections of the Irkutsk amphitheatre were studied by Karatajute-Talimaa and Valiukevicius; in 1984 sections of the Niuya-Beresovo district in the S Yakutia were studied; and in 1986 sections of the Maimetcha district in the southern part of the Taimyr peninsula were studied (Karatajute-Talimaa took part in the sampling during the last two field seasons).

2. Geological distribution

Stratigraphic zonation of the E Siberian palaeobasin was presented in Karatajute-Talimaa & Predtechenskyj (1995, fig. 1). Later the new improved version involving division into subregions and districts was used, as elaborated by Tesakov *et al.* (1998, fig. 1) and Tesakov (1999).

The stratigraphical subdivision, based on the distribution of facies, includes five subregions and fifteen districts. The scales of acanthodians were discovered in five districts and areas (see Figs 1, 2): II—North Priyenissey subregion, Turukhansk district; III—Pritunguska subregion, Kochumdek district (Tunguska area); IV—Niuya—Beresovo subregion and district; V—Irkutsk subregion, Ilim (Angara–Ilim area) and Balturino (Tchuna–Biriussa area) districts.

A more exact dating of formations was also made and the whole sequence of the Balturino Formation (beds 1–62) is now attributed to Lower Silurian (Llandovery). Beds 63 and 64 with microremains of vertebrates are assigned to the lower part of the Barmo Formation (lowermost Sheinwood)—see Tesakov (1999, table I).

In the Silurian of the Central Siberian basin, open deep shelf, open shallow shelf, belt of bars, restricted shallow shelf, lagoonal, and coastal facies have been studied (Predtechenskyj 1989). Microremains of vertebrates have been determined in the bar belt facies, in the shoaly part of the restricted shallow shelf, in deposits of saline lagoons and in the beach and submarine–deltaic facies of the coastal belt (Karatajute-Talimaa & Predtechenskyj 1995, fig. 2).

The main sampling for vertebrate microremains, including acanthodian scales, was carried out in the Melichan and Utakan Formations of the Niuya–Beresovo district (IV), the Rassokha Formation of Ilim district V_j and the Balturino Formation of Balturino district V_2 (see Figs 1, 2).

Lower Silurian deposits in the Niuya–Beresovo district IV_1, investigated in 1984, were sampled for dissolution from twelve outcrops on the banks of the Niuya River and two outcrops of the Lena River. The correlation of the sampled sections and the distribution of recovered vertebrate microremains is given in Karatajute-Talimaa & Predtechenskyj (1995, fig. 6). More numerous, but very small, scales of thelodonts, chondrichthyans (?) as well as acanthodians (*Lenacanthus priscus* gen. et sp. nov.—defined below) have been discovered in deposits of the Melichan Formation (Moyerokanian Regional Stage, Lower Llandovery). These were in the lower part of outcrops 147 and 156, and in deposits of the Lower Utakan Subformation (upper part of outcrops 149 and 156, 152 and 157 of the Niuya River and 164 on the bank of the Lena River), ascribed to the Khaastyrian Regional Stage, Middle Llandovery. A few vertebrate remains have been found in the Upper Utakan Subformation (Agidyian Regional Stage, Upper Llandovery) in outcrop 150, bed 1. Nevertheless, some scales of the genus *Tchunacanthus* have been determined amongst them. Acanthodian scales have been discovered in deposits of the Niuya Formation (Khakomian Regional Stage, Wenlock), but these could only be defined to genus (outcrop 151 and uppermost part of outcrop 158).

In the Ilim district (V_1), vertebrate remains have been discovered at Tushama in quarries along the bank of Nazarovskaya Rassokha River (outcrop 141, beds 19–43 and above bed 43 in coastal debris). This part of the section corresponds to the middle and upper parts of Rassokha Formation; after Tesakov (1999) these could be ascribed to the Middle and Upper Llandovery Substages (see Fig. 2). The acanthodian scales (*Lenacanthus priscus* gen. et sp. nov.) have been found in the Middle Llandovery (bed 24). Scales of *Tchunacanthus* sp. have been found in the uppermost part of the section, in coastal debris above bed 43.

In the Balturino district (V_2), Lower Silurian deposits of the Balturino Formation crop out 3 km above the village of Staroe Balturino (outcrop 135); the best are on the right bank of the Tchuna River. In the upper part of the section, in the 45 m-thick deposits of the Upper Balturino Subformation (beds 43–49), numerous vertebrate microremains have been found with acanthodian scales dominant, both in frequency and quantity. The Balturino Formation is ascribed to the Llandovery. The uppermost part of the section in outcrop 135 (beds 63, 64) must be ascribed to the Barmo Formation (Agidyian Regional Stage, Wenlock; see Fig. 2).

Besides the enumerated materials, acanthodian scales have been found in the following localities: N Prienissey subregion (II)–Turukhansk district (II_2), in borehole Yass-4 of the Yassenga area at a depth of 1059·7 m (*Tchunacanthus* sp.). Scales of *Tchunacanthus* sp. have been found in borehole N-1 of the Noginsk area at a depth of 851·8 m (Lower Uragdan Subformation, Khakomian Regional Stage, Wenlock).

In the Pritunguska subregion III, Kochumdek district (III_1), on the bank of the Nizhniaya Tchunku River in Kulinna Formation (Khaastyrian Regional Stage, Middle Llandovery), scales of *Lenacanthus priscus* have been found together with the index thelodont *Loganellia sibirica* (Kar.-Tal.) and *Angaralepis moskalenkoae* (Kar.-Tal.).

The entire microvertebrate collection, described above, was transferred to us by Dr Moskalenko (Novosibirsk).

Acanthodian scales have also been found in nearshore marine deposits of the adjacent Tuva–Mongolian Lower Silurian palaeobasin. Well-preserved scales of *Tchunacanthus* sp. indet. were discovered in Tuva (Russia), in deposits of the Kyzyl–Tchiraa Formation in the Kyzyl–Tchiraa section, sample 702, attributed to the Middle Llandovery by Kulkov *et al.* (1985, fig. 4) or to the late Llandovery by Vladimirskaya *et al.* (1986).

In northwestern Mongolia, at the same age level (Khutsyn–Bulak beds, Upper Llandovery), scales of *Tchunacanthus obruchevi* are present together with exoskeletal microremains (scales and tesserae) of thelodonts, heterostracans, chondrichthyans, mongolepidids and anaspids (?) (Rozman coll., Moscow; Khosbayar and Sodov coll., Ulan-Bator). Samples containing numerous vertebrate microremains have been picked from the Lower Silurian key section, located 80 km northwards from Lake Khara-us-Nur, on the southeastern slope of Tchagartai mountains (Karatajute-Talimaa *et al.* 1990).

It is worthy of note that in over 300 samples, prepared for dissolution to obtain the separated microremains, more that 100,000 scales were found but none with morphology that could represent a spine, or a tooth, in the entire collection.

O_3	Landoverian			Wenlockian	GLOBAL SERIES
	Rhuddan	Aeron	Telych.	Sheinw.Homer	STAGE
	Llandovery			Wenlock	Regional series
	Moyerocanian	Khaastyrian	Agidyan	Khakomian	Regional Stage (Regional units for Siberian Platform)
	Moyerocan	Khaastyr	Agidy	Khakoma	Formation (Regional units for Siberian Platform)
	Lower Upper	Lower Upper	Lower Upper	Lower Upper	Subformation (Regional units for Siberian Platform)
Formation	Chamba	Tal ikit	Omnutakh	Uragdan	SIBERIAN PLATFORM; North Prienissey Subregion II; Turukhansk district II_2
			Tchuna-canthus obruchevi	*Tchuna-canthus* sp. indet.	
Formation	Kochumdek	Kulinna	Razvilka	Usas	SIBERIAN PLATFORM; Pritunguska Subregion III; Kochumdek distric III_1
		Lena-canthus priscus		*Tchuna-canthus* sp. indet.	
Formation	Melichan	Utakan		Niuya	SIBERIAN PLATFORM; Niuya-Beresovo Subregion IV; Niuya-Beresovo district IV_1
Subformation	L. U.	L.	M. U.	Lower Upper	
	Lenacanthus priscus	*Lenacanthus priscus*	*Lenacanthus priscus*	*Tchuna-canthus ?* sp. indet.	
nos outcrop-bed	155/1-156/12; 156/13-156/28	156/29-38-157/23	157/24-42-159/7; 159/7 158/5	158/5-151/18	
Formation	Rassokha			Deshyma	SIBERIAN PLATFORM; Irkutsk Subregion V; Ilim district V_1
Subformation	L.	M.	U.		
		Lena-canthus priscus	*Tchuna-canthus obruchevi*		
nos outcrop-bed	141/3-22	141/23-38	141/39-48		
Formation	Balturino			Barmo	SIBERIAN PLATFORM; Irkutsk Subregion V; Balturino district V_2
Subformation	L.	M.	U.		
	Tchuna-canthus? sp. indet. Acanthodii n.g.	Acanthodii indet.	*Tchuna-canthus obruchevi* Acanthodii n.g.	*Tchunacanthus obruchevi* (?)	
nos outcrop-bed	135/1-22	13 5/23-41-42	135/43-62	135/63,64	
Formation	Alash	Kyzyl-Tchiraa	Angachi	Dashtygoj	TUVA
		Tchuna-canthus sp. indet.			
Bed	Khutsyn-Bulak				NW MONGOLIA
			Tchuna-canthus obruchevi		

Figure 2 Distribution of acanthodians in the Lower Silurian of the Siberian Platform, Tuva (Russia) and NW Mongolia. Stratigraphical distribution after Tesakov (1999, table I) and Vladimirskaya *et al.* (1986). Distribution of vertebrates in outcrops and beds (see Karatajute-Talimaa & Predtechenskyj 1995, figs 3, 6).

3. Systematic palaeontology

Subclass Acanthodii Owen, 1846
Order Tchunacanthida Kar.-Tal. et Smith ordo nov.

Diagnosis. Micromeric growing scales: head, transitional and body; also larger scales, possibly tesserae, with complex crown morphology; areal, areal-superpositional and super-

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positional growth (see Karatajute-Talimaa 1998) of crown characteristic of squamation of each part of body; head scales with smooth crown, or with concentric lines of growth on surface; sculptured anterior crown, consisting of longitudinal ridges, characteristic of transitional and body scales; base shallow, or reaching a considerable depth, particularly in head and transitional scales; scales of all morphological varieties notable for their great density, and absence of canal system; crown composed of special cellular mesodentine, with unipolar cell cavities, each with short and very thin, branched dentine tubules, unlike cells in scale base; both crown and base regions show first and second growth sequences.

Composition. Family Lenacanthidae fam. nov. and Family Tchunacanthidae fam. nov.

Fam. Lenacanthidae Kar.-Tal. et Smith fam. nov.

Diagnosis. The same as the genus by monotypy (see below).

Composition. One genus *Lenacanthus* gen. nov.

Genus *Lenacanthus* Kar.-Tal. et Smith gen. nov.

Etymology. Named after the Lena River and *akantha* (in Greek, spine, thorn).

Type species. *Lenacanthus priscus* sp. nov., Lower Silurian, Lower and Middle Llandovery, Moyerocan and Khaastyr Formations. Southern Yakutia (Niuya–Beresovo Subregion, Niuya–Beresovo District) Melichan Formation and Lower Utakan Subformation. Irkutsk amphitheatre (Irkutsk Subregion, Ilim District), Middle Llandovery, Kulinna Formation (see Figs 1, 2).

Diagnosis. Same as species by monotypy (see below).

Composition. One species.

Comparisons. The presence of head, transitional and body scales in the squamation brings together both genera, *Lenacanthus* and *Tchunacanthus*. Also the special mesodentine with distinct small cells (odontocytes) present in the scale crown is characteristic of both genera. Canals are not found in either the crown or the base of these genera. Small differences are apparent in the extent of crown lamination. The typical areal growth of the crown, so characteristic of head, transitional and some body scales of the genus *Tchunacanthus*, occurs only on the head and partly on the transitional scales of the genus *Lenacanthus*. The concentric growth lines are generally not seen at all, except on the crown surface of *Lenacanthus* head scales, whereas they stand out distinctly on the surface of the head and transitional scales of the genus *Tchunacanthus*. The sculpture differs greatly on the crowns of transitional scales from that on the body scales of these genera. The base of all morphological types of scales of *Lenacanthus* is flat, or only slightly convex, and never reaches a significant height, as is characteristic for the scales of the genus *Tchunacanthus*. Thinner growth layers of the second phase are developed in both the crown and the base in the genus *Tchunacanthus* and appear to be absent in scales of *Lenacanthus*. Scales in the Tchunacanthida, including the genus *Lenacanthus*, differ from the Climatiida (genera *Nostolepis*, *Cheiracanthoides*, *Laliacanthus*, *Minioracanthus*) by the absence of any trace of vessel canals. They also differ in the type of mesodentine in the crown, by the growth type of the crown, and in the presence of special head scales (also see comparison in the description of the genus *Tchunacanthus*). *Tchunacanthus* and *Nostolepis* are similar in that they both have scale-tesserae, but *Lenacanthus* does not.

Geological and geographical range. Scales of the genus *Lenacanthus* are widespread in the Lower and Middle Llandovery, Moyerocan and Khaastyr Formations; S Yakutia (Niuya–Beresovo Subregion, Niuya–Beresovo District) Melichan Formation and Lower Utakan Subformation; Irkutsk amphitheatre (Irkutsk Subregion, Ilim District), Middle Llandovery, Kulinna Formation (see Figs 1, 2).

Lenacanthus priscus Kar.-Tal. et Smith sp. nov.
Figures 3–9

Etymology. From the Latin *priscus*, meaning ancient.

Holotype. Institute of Geology, Lithuania, body scale no. 10-101 (Fig. 5F), S Yakutia, River Niuya, outcrop 156, bed 37, Lower Silurian, Middle Llandovery, Lower Utakan Subformation.

Diagnosis. Very tiny scales (length up to 1·5–2·0 mm)—head, transitional and body scales distinguishable; head scales irregular, polygonal, seldom hexagonal, and rounded, with flat, or gently convex, smooth crown; edges of crown with relatively deep hollows and notches; neck feebly demarcated; base mirroring crown in form and extent, low, relatively flat but slightly convex; primordial area of the crown in some, polygonal; transitional scales irregular; scales broad and short; anterior crown subdivided into two, four or seven sections, belonging to transitional type; transition of crown into base gradual; base smaller than crown, low, polygonal or oval/diamond-shaped, with crown extended backwards to point; crown anteriorly subdivided into 3–5 sections by deep, longitudinal fissures; base low, flat or barely convex; areal (head), areal-superpositional (transitional) and superpositional (body) scale growth; crown of cellular mesodentine with distinct lacunae and very thin, branched tubules; base with simple cells, lacunae without branching canaliculi; system of vascular canals absent.

Description; morphology. Scales are very small: 0·2–0·6 mm in length, 0·1–0·6 mm in width. There are several varieties of the crown in head, body and transitional scales, but each of the morphological peculiarities is clearly distinguished. It is easy to establish a morphological set by tracing the gradual morphological alteration of the crown from head to typical body scales (Figs 6, 7).

Head scales. These have rather complex outlines, from polygonal (hexagonal) with slightly concave or convex edges,

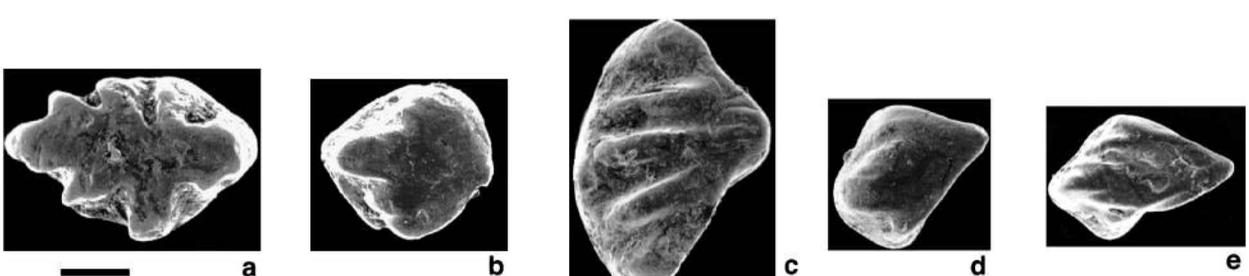

Figure 3 *Lenacanthus priscus* gen. et sp. nov.: (a) head scale in crown view; (b, c) transitional scales in crown view; (d, e) body scales in crown view. LIG 10-128 to 10-132. South Yakutia (Russia), Niuya-Beresovo Subregion IV, Niuya-Beresovo District IV1, Lower Melichan Subformation, Lower Llandovery, Lower Silurian (see Figs 1, 2). Scale bar ⊃ 250 μm.

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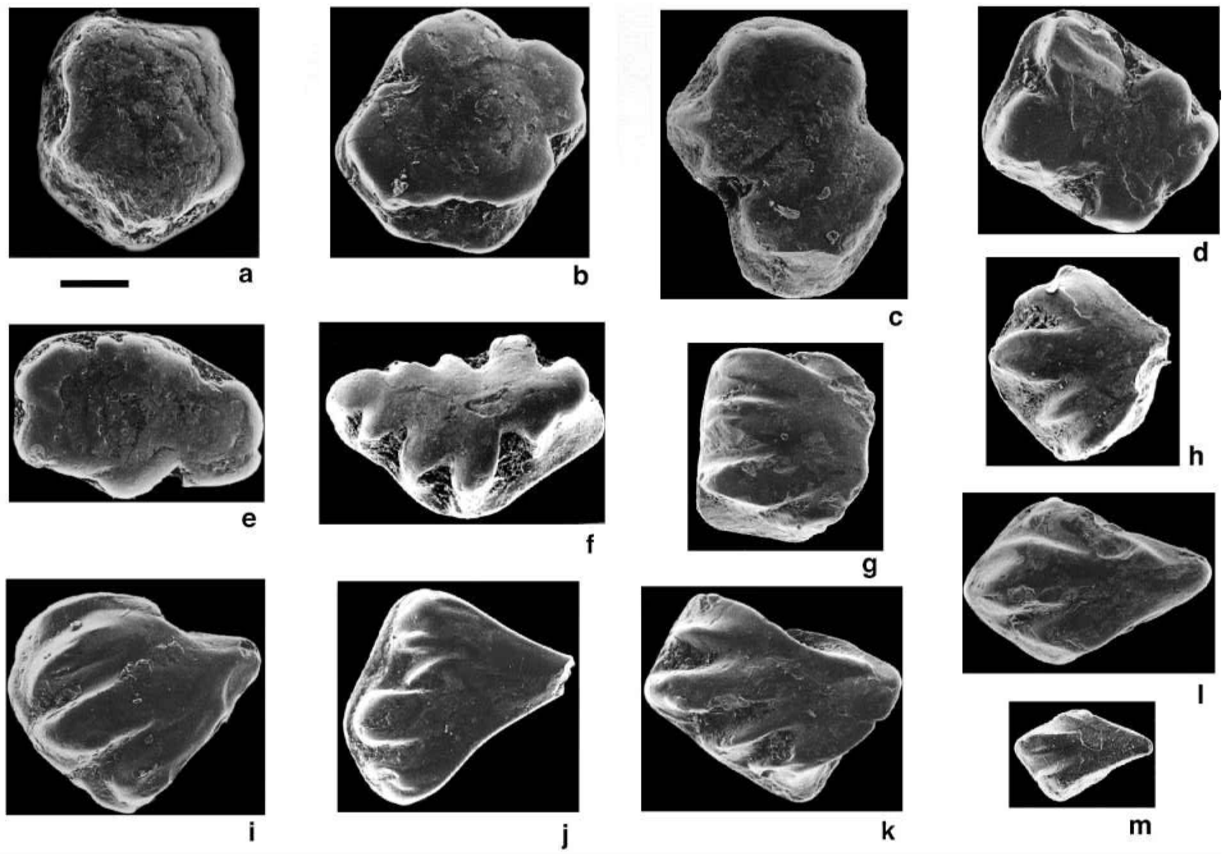

Figure 4 *Lenacanthus priscus* gen. et sp. nov.: (a–f) head scales in crown view; (g–i) transitional scales in crown view. LIG 10-133 to 10-145. South Yakutia (Russia), Niuya-Beresovo Subregion IV, Niuya-Beresovo District IV1, Lower Utakan Subformation, Middle Llandovery, Lower Silurian (see Figs 1, 2). Scale bar ⊃ 250 μm.

to monolithic (Figs 4a–c; 5a; 6a; 7e), to scales with more complex crown outlines, sometimes elongated, with deep hollows and notches (Figs 3a; 4d–f; 5b, c; 6b, c; 7a–d, f, g). The crown is low, flat and smooth, and on the surface concentric growth lines, characteristic of all head scales, can be discerned (Fig. 4a). The neck is poorly marked and the transition from crown to base is gradual. The base has the same common outline as the crown, and is low and flat, or, more seldom, slightly convex. Head scales were apparently distributed in a tight mosaic arrangement because the sides of the bases are very often almost vertical.

Transitional scales. These are diamond-shaped or oval, wider than they are long, with short but deep hollows anteriorly (Figs 3b, c; 4g–i; 5d, e; 6d–i; 7h, i); anteriorly they

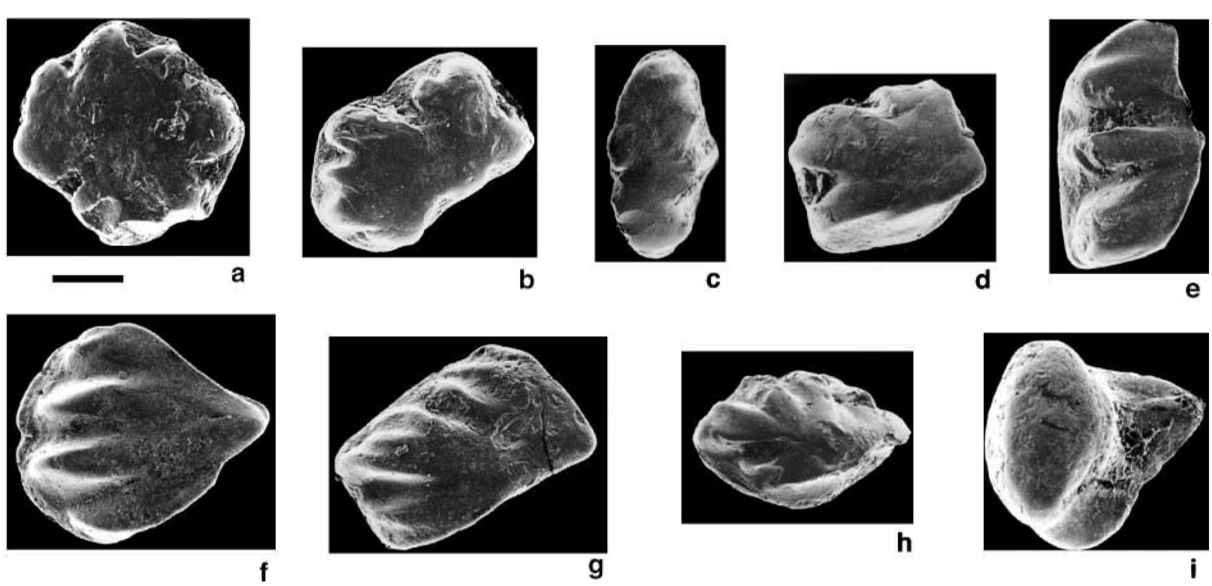

Figure 5 *Lenacanthus priscus* gen. et sp. nov.: (a–c) head scales in crown view; (d, e) transitional scales in crown view; (f) holotype, body scale in crown view, LIG 10-151; (g, h) body scales in crown view; (i) body scale in basal view. LIG 10-146 to 10-154. South Yakutia (Russia), Niuya-Beresovo Subregion IV, Niuya-Beresovo District IV1, Niuya River, outcrop 156, beds 37, 38 Lower Utakan Subformation, Middle Llandovery, Lower Silurian (see Figs 1, 2). Scale bar ⊃ 250 μm.

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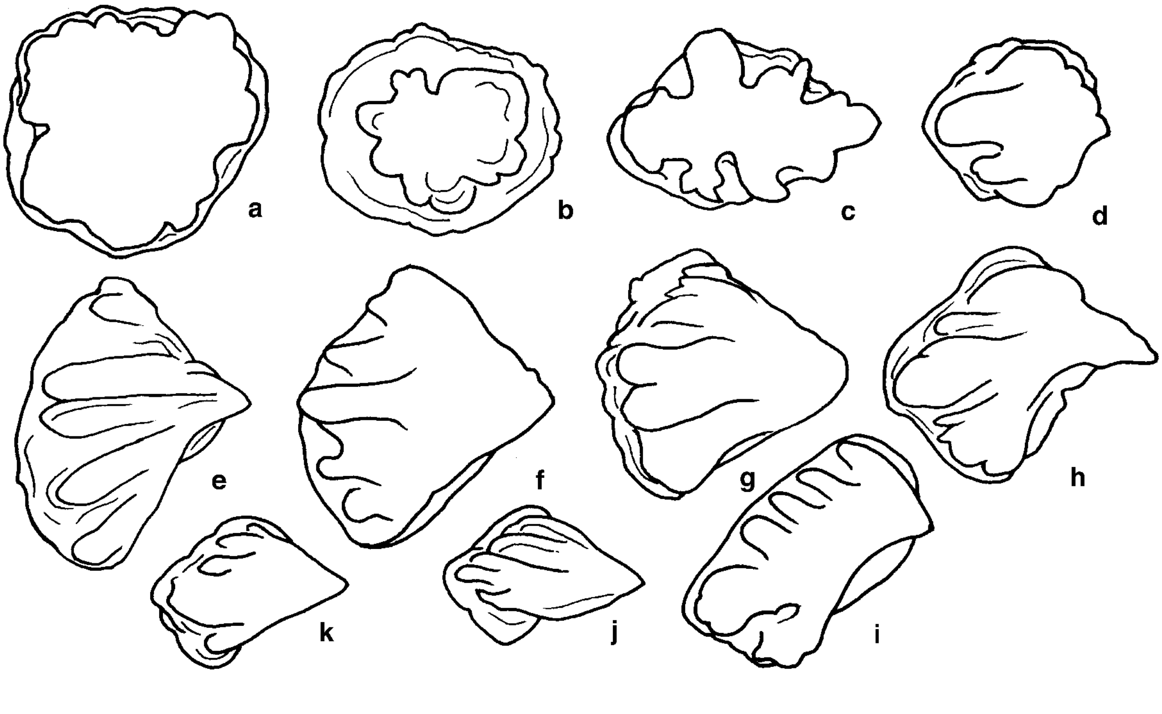

Figure 6 *Lenacanthus priscus* gen. et sp. nov.: morphological set of scales from the lower level of outcrop 156 (bed 3) of Niuya River in South Yakutia: (a–c) head scales; (d–i) transitional scales; (j–k) body scales. LIG 10-112; 10-111; 10-128; 10-129; 10-130; 10-108; 10-106; 10-109; 10-107; 10-131; 10-132. Lower Melichan Subformation, Lower Llandovery, Lower Silurian (see Figs 1, 2). Scale bar $\supset 250\,\mu$m.

have 3–5 long ridges. The medial (central) ridge is usually the largest, and extends forward. The posterior edge of the crown of such scales is smoothly rounded, or has a weak point. The crown of transitional scales is high, larger than the base, and slightly displaced backwards. The base is low, diamond-shaped or oval, elongated and slightly convex.

Body scales. The crown is irregular but diamond-shaped, wider anteriorly, and wedge-shaped posteriorly, going to a point (Figs 3d, e; 4j–m; 5f–i; 6j–k; 7j–m). Sculptural elements of longitudinal ridges, separated by deep furrows, reach only to the middle part of the crown, and are relatively coarse compared to the usual size in scales. Most body scales contain a wider medial area and 1–2 pairs of lateral ridges. The anterior edge is quite often separated into two areas by a short longitudinal furrow, which breaks up the general outlines of the crown. The posterior surface of the crown of body scales is

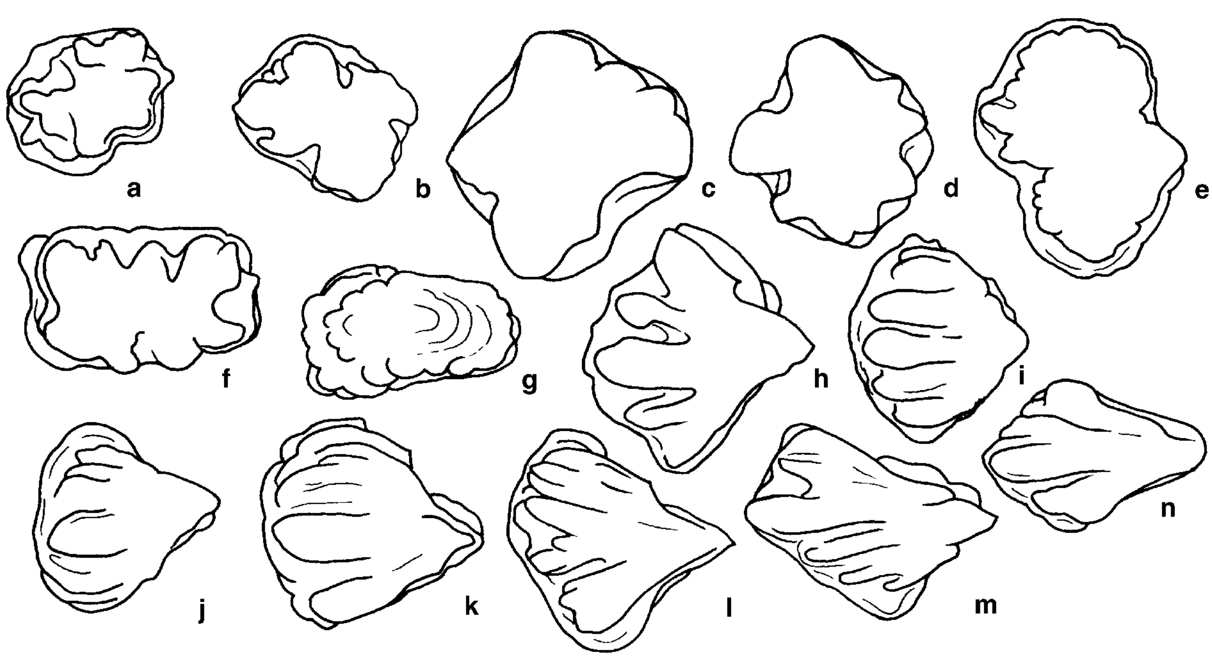

Figure 7 *Lenacanthus priscus* gen. et sp. nov.: morphological set of scales from the lower level of outcrop 156 (bed 37) of Niuya River in South Yakutia: (a–g) head scales; (h, i) transitional scales; (j–n) body scales. LIG 10-155; 10-156; 10-134; 10-136; 10-35; 10-406; 10-439; 10-440; 10-441; 10-141; 10-442; 10-142; 10-143. Lower Utakan Subformation, Middle Llandovery, Lower Silurian (see Figs 1, 2). Scale bar $\supset 250\,\mu$m.

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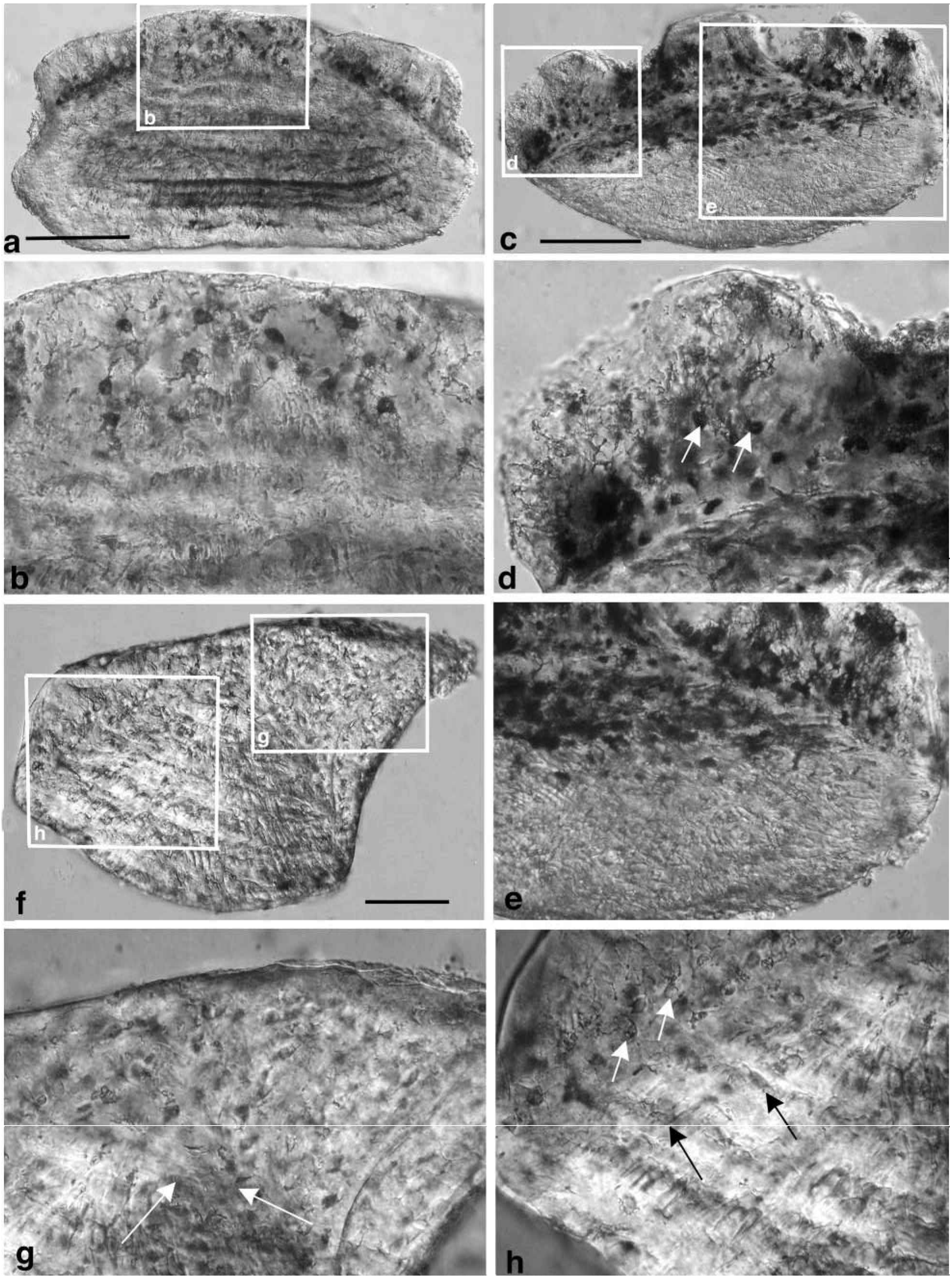

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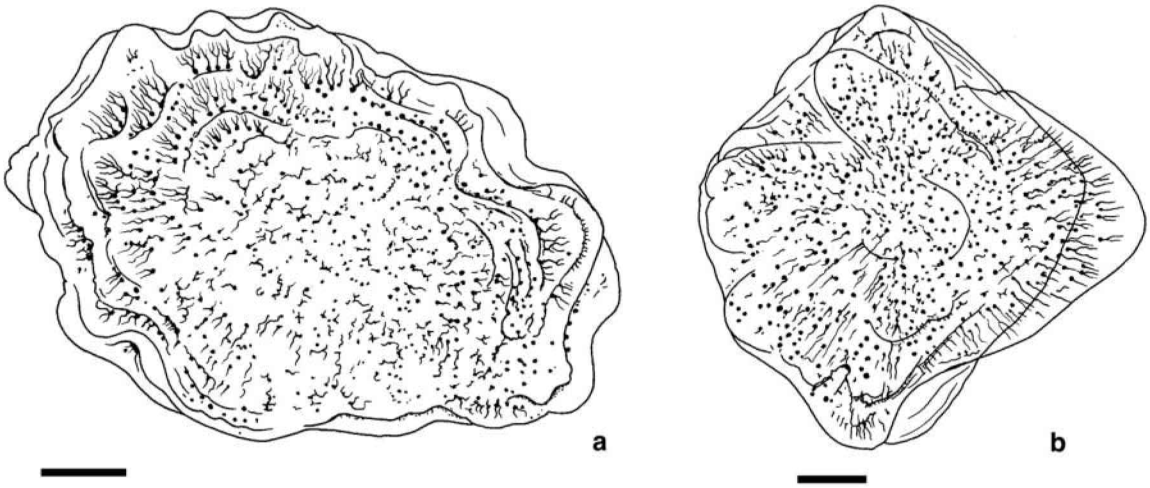

Figure 9 *Lenacanthus priscus* gen. et sp. nov.: (a) coronal part of head scale in horizontal section, areal growth layers each consisting of mesodentine, shows radial arrangement of mesodentine tubules; (b) coronal part of body scale in horizontal section, the orientation of the mesodentine cells and tubules is clear in the posterior part. LIG slide nos. 1232, 1227. South Yakutia (Russia), Niuya-Beresovo Sub-region IV, Niuya-Beresovo District IV1; Niuya River, outcrop 156, bed 37, and outcrop 157, bed 37, Middle Utakan Subformation, Middle Llandovery, Lower Silurian (see Figs 1,2). Scale bars 150 μm.

flat and smooth. The base is considerably smaller than the crown, diamond-shaped or oval, and slightly convex.

Histology. Horizontal and vertical sections (more than 20 microsections) allowed the type of growth of the crown to be determined, in scales of different morphological varieties, and also allowed variation of the tissue structure to be observed (Figs 8, 9).

In a horizontal section of the crown of a head scale, in which growth by apposition increases the area of the scale, the growth layers are very apparent, as represented in Figure 9a. Each concentrically distributed growth zone is not even in width, and this may account for the crown asymmetry. These growth zones, separated by lines, are not present in the central part of the crown (scale primordium). Small round cavities for the cell bodies (odontocyte lacunae) are obvious in each growth zone and each lacuna leads into a thin, unipolar tubule with small, dichotomous tubuli. The lacunae with diverging tubules represent a polarised cell type (Fig. 9a); although regularly arranged in the concentric growth layers, they are scattered in the central coronal tissue of both head and body scales (Figs 8b, d, 9a). Very few lacunae can be seen in the narrower growth layers.

Cell lacunae are sparse in the basal tissue but distributed in horizontal rows parallel to the lamellae (Fig. 8h) of the base. Lacunae are most numerous in the central, coronal part of the base (Fig. 8c, d, e). Usually the small lacunae are difficult to distinguish because, first and foremost, the coarse Sharpey's fibre spaces are disposed radially (Fig. 8e–h) and these can be misidentified in cross-section as cell spaces. The growth lines are not numerous and do not stand out very clearly.

The inner structure of transitional scales is identical to that of head scales. Sometimes growth zones increase the area of the scale, and these can be seen in the anterior section of the crown, where the short longitudinal ridges are developed, but in the posterior part growth regions are usually superimposed to give thickness to the crown. In the base, the linear spaces of the Sharpey's fibres are most sharply marked and closely packed, so that growth lines are only traced for short distances between them (Fig. 8a, h).

The superpositional type of growth is characteristic of body scales (Fig. 8c, f). However, the growth laminae in the central part of the crown are very thin, or not even complete. The mesodentine of each growth layer is very distinct, where thin, branching dentine tubules emerge from small round cavities: odontocyte lacunae (Fig. 9a). In a horizontal section of the crown of body scales (Fig. 9b) the disposition of the cells and tubules is clear. The great number of cell spaces is striking, as is the distal polarity of the numerous tubules. Growth layers with more regular distribution of odontocyte spaces are seen in Figure 9a. Thin, straight, but radial spaces of Sharpey's fibres are seen distinctly in the anterior part (Fig. 8e, f, h). The base of the body scales is slightly convex, reflected by the course of the growth lines. The upper part of the basal cone, so characteristic for scales of other acanthodian genera, is quite low with a smooth apex. The cell spaces are very small and not always distinct, but are distributed in the upper part of the basal cone (Fig. 8c, e–g), or disposed parallel to growth lines (Fig. 8h). The first growth areas can be traced in the base in all examined sections. They are almost horizontal but slightly curved downwards (it depends on the degree of convexity of

Figure 8 *Lenacanthus priscus* gen. et sp. nov.: (a, b) head scale, vertical transverse section, crown consisting of central primordial part with large mesodentine cells (area of b inset) and 2–3 pairs of lateral areal growth regions; basal tissue with few cells, many growth layers and radial Sharpey's fibre spaces; (b) enlarged coronal tissue from inset in (a), mesodentine with irregular cell arrangement and tubules (odontocytes), also upper part of basal tissue without these cells, showing rare cell lacunae, growth layers and perpendicular to these Sharpey's fibre spaces LIG 1337; (c, d, e) body scale, vertical transverse section, central primordial scale with two additional growth zones (most lateral zone, high power in (d); right side crown and base in (e), all show the contrast between mesodentine in the crown (odontocytes white arrows), cellular bone in the base with a high cell density at the apex, and fewer cells but more Sharpey's fibres in the more basal part. LIG 1199; (f, g, h) body scale in vertical longitudinal section, with steep apex to base (g), radial Sharpey's fibres in all the basal tissue and (h) contrasting cell types in the mesodentine (odontocytes—white arrows) and few osteocytes in the basal bone (black arrows). LIG 1338. South Yakutia (Russia), Niuya-Beresovo Subregion IV; Niuya-Beresovo District IV1; Niuya River, outcrop 157, bed 37; Middle Utakan Subformation, Middle Llandovery, Lower Silurian (see Figs 1, 2). Scale bars ⊃ 250 μm.

the base). The spaces occupied by Sharpey's fibres are perpendicular to the growth lines and radial to the basal surface (Fig. 8f). Usually, they are particularly well developed in the more basal laminae, where there would have been functional attachment and thicker unmineralised cores to the fibre bundles.

Observations. The description of *Lenacanthus priscus* scales is taken from material from S Yakutia (Niuya River). Scales of this species, found at other places, are not so numerous and most often they are rounded by an artefactual process. Sizes of scales and their general morphology fully correspond to those described above. In sample 141/24 (Tushama, quarries, Ilim District V_1), the morphological set of scales is almost complete and includes head scales.

Material. The collection of *L. priscus* scales from the River Niuya outcrops contains about 300 well-preserved scales of light yellow-brown colour, yielding good sections. The collection with most numerous scales (about 50) is found in samples 141/24 and 141/26 from the outcrop near Tushama station (Ilim District).

Family. Tchunacanthidae Kar.-Tal. et Smith fam.nov.

Diagnosis. The same for the genus by monotypy (see below).
Composition. One genus, *Tchunacanthus* gen. nov.

Genus *Tchunacanthus* Kar.-Tal. et Smith gen. nov.

Etymology. After the Tchuna River (Uda) in the S Krasnoyarsk District, and *akantha* (Greek for spine, thorn).

Diagnosis. Same as species by monotypy (see below).

Type species. *Tchunacanthus obruchevi* Kar.-Tal. et Smith sp. nov., Lower Silurian, Upper Llandovery of Irkutsk amphitheatre and northwestern Mongolia.

Composition. The type species, and *Tchunacanthus* sp.indet.

Comparison. Among Silurian acanthodians, only scales of the Climatiida (genera *Nostolepis* and *Cheiracanthoides*) have bone cells in the basal scale tissue. The scales of the genus *Tchunacanthus* resemble those of *Cheiracanthoides* and, partly, *Gomphonchus* (*G. sandelensis*) of the order Ischnacanthida, in the crown sculpture of some of the body scales. Head scales with areal growth of the crown are not found in the squamation of known genera of acanthodians. Scales of this type are peculiar only to the two most ancient genera, *Lenacanthus* and *Tchunacanthus*. Areal growth of the crown is more a characteristic of scales of Actinopterygii (genus *Cheirolepis*), some elasmobranchs, and modified acanthodian scales of *Nostolepis robusta* Gross type. It is necessary to stress that areal growth zones in the head scales of *Lenacanthus* and *Tchunacanthus* are complete around the crown perimeter, and not interrupted, as, for example, in elasmobranch scales of the *Holmesella* type (Ørvig 1966). Areal growth in the crown is also characteristic of the transitional and some body scales of the genus *Tchunacanthus*. On these grounds, *Tchunacanthus* differs not only from the scales of Nostolepidida, but also from *Lenacanthus*. In the crowns of Nostolepidida and representatives of other acanthodian orders, the mesodentine has a well-developed system of dentine canals (Gross 1971; Valiukevičius 1985). In the proximal areas of each coronal growth zone, nostolepid scales have canals into which the apertures of dentine tubules open. Tchunacanthid scales have no canal system at all, only one row of simple cell spaces, giving rise distally to fine branches of the tubules. Such a mesodentine type is quite different from the tissue of the scale base and is found also in the crown of *Lenacanthus*. Head scales in *Tchunacanthus* have a smooth crown and, notably, a deep base (in adult and old scales), in the centre of which is a depression. Outwardly, such scales resemble the head scales of thelodonts, but the depression does not open into a pulp cavity; moreover, the growing base has a definite acanthodian structure.

Growth laminae of the first and second order, so characteristic of scales and tesserae of the genus *Tchunacanthus*, are also established in nostolepidid scales (J. Valiukevičius, pers. comm.).

Geological and geographical range. The scales of the genus *Tchunacanthus* occur in the Upper Llandovery deposits (Agidyan Regional Stage), and in Lower Wenlockian deposits (Khakomian Regional Stage), N Prienissey Subregion, Turukhansk District (II_2), Omnutakh and Uragdan Formations, Pritunguska Subregion, Kochumdek District (III_1), Usas Formation, Niuya-Beresovo Subregion, Niuya-Beresovo District (IV_2), Lower Niuya Subformation, and Irkutsk Subregion, Ilim District (V_1), Upper Rassokha Subformation.

In the Balturino District (V_2) the scales and scale-tesserae of *Tchunacanthus* are found in the entire sequence of the Balturino Formation (Llandovery) and in the lower part of the Barmo Formation (Lower Wenlock).

Scales of *Tchunacanthus* sp.indet. were discovered in Tuva (Russia), in deposits of the Kyzyl–Tchiraa Formation (Middle Llandovery), while scales of *Tchunacanthus obruchevi* occur in northwestern Mongolia (Khutsyn-Bulak beds, Upper Llandovery: see Figs. 1, 2).

Tchunacanthus obruchevi Kar.-Tal. et Smith sp. nov.
Figures 10–12; 13a–k; 14–19

Etymology. In honour of Professor Dmitrij Vladimirovich Obruchev, who was the first to point out the presence of acanthodian scales in the Lower Silurian of the Irkutsk amphitheatre.

Holotype. Lithuanian Institute of Geology, body scale 10–517 (Fig. 12m), Balturino District, River Tchuna, Staroe Balturino outcrop (135), talus of beds 43–49; Lower Silurian, Upper Llandovery, Upper Balturino Subformation.

Diagnosis. Range of morphological variation, attributed to topological position in the squamation; head, transitional and body scales, larger tesserae, complicated sculptured crowns, all multilobate shapes; head scales, smooth crown with distinct concentric growth lines; transitional body scales, crown surface folded into longitudinal ridges, formed of separate tubercles; growth lines traced on posterior section; base of head and transitional scales deep, with funnel-shaped or oblong furrows in centre; surrounding convex bosses subdivided by narrower furrows; base of body scales proportionally less than crown, diamond-shaped, convex; areal growth type characteristic of head and transitional scales; growth both areal-superpositional, only superpositional, on body scales; scale varieties very dense tissues; canal system absent; crown cellular mesodentine, with regular, rounded cell spaces, proximal in each dentine layer; base contains simple, small, fusiform, cell spaces without processes, disposed parallel to growth lines; distinct growth lines, first order, very thin second-order lines; alternating Sharpey's fibre bundles, fibre tubules evident.

Description; morphology

Head scales. The common form is diverse, varying from a regular hexagon, with well-expressed angles and faces of the crown, almost of the same length (Fig. 10a–c; 14q), to elongated polygonal crowns, irregular in form, with convex or concave faces (Fig. 10e–h, j–l; 14r). Some scales are almost round, with smooth angles, and irregularly pentagonal, or an

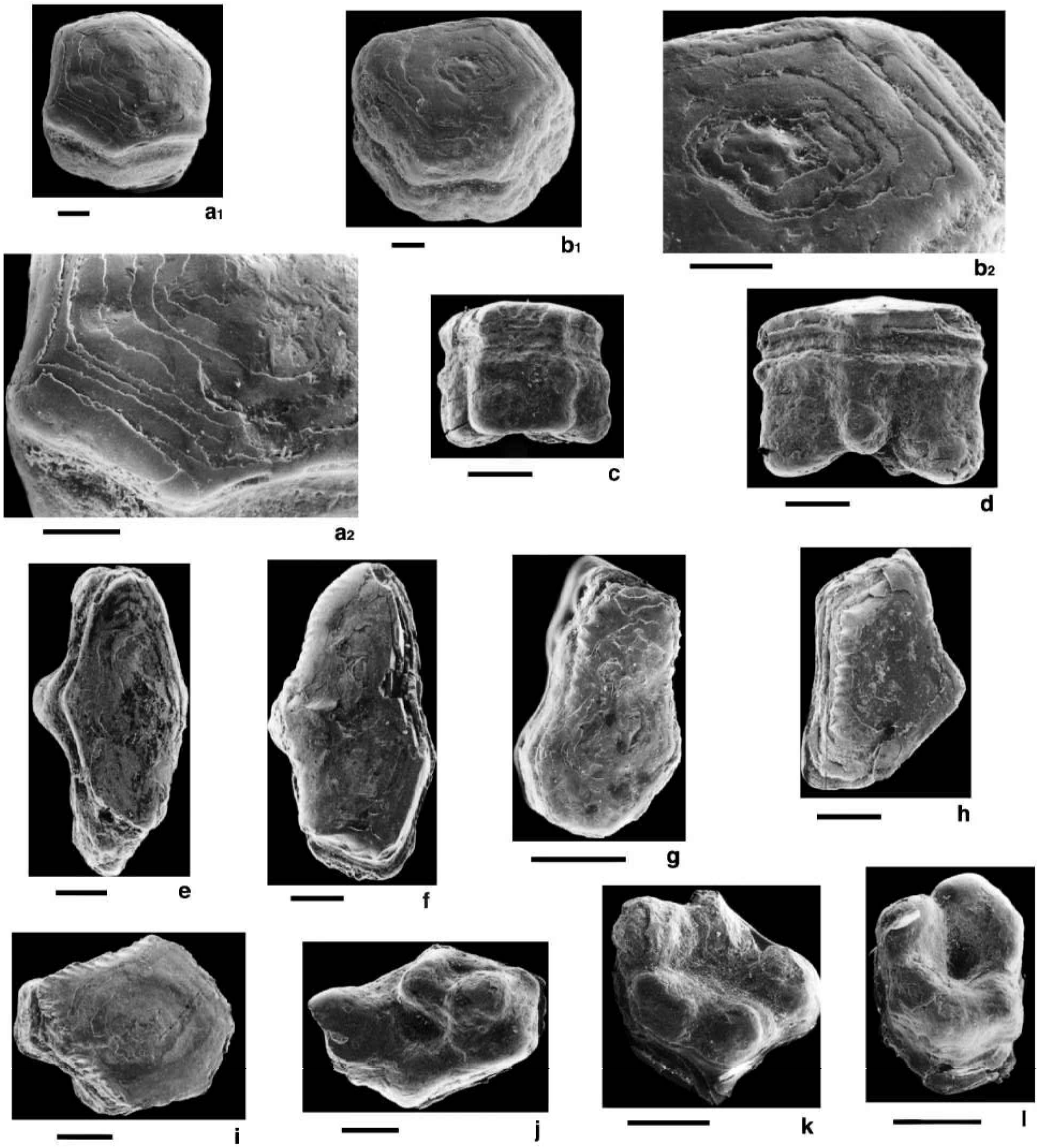

Figure 10 *Tchunacanthus obruchevi* gen. et sp. nov.: a_1, b_1 hexagonal head scales in crown view, a_2 and b_2 enlarged to show growth zones and overlap of later coronal layers; (c, d) head scales in lateral view; (e, f, g, h,) transversely extended head scales; (i) transitional (?) scale in crown view; (j, k, l), head scales in basal view showing depression in middle part of base with surrounding elevations (tuberosities). LIG 10-403, 10-500 to 10-510. South Siberia, Irkutsk Subregion V, Balturino district V2, Tchuna River, outcrop 135, beds 43–49; Upper Balturino Subformations, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bars $\supset 250\,\mu$m.

elongated oval in shape. The size of head scales varies from 1·5 mm to 0·45 mm in diameter. Large scales, up to 2·0 mm, can be found. The crown is slightly convex with gentle slopes and a smooth surface (Figs 10a–g; 13a), or, infrequently, with relatively low fine-notched edges (Figs 10c, d, f; 13a), merging with the neck through a sharp border. The main crown surface is smooth, without sculpture, but with distinct concentric growth lines (Fig. 10a, b). The growth lines of most head scales are so clear that it is possible to find the location of the central primordial area and thus to calculate the total number of growth layers adding to the area of the scale. The neck is low but distinct and expressed in the form of a groove around the whole perimeter of the scale (Fig. 10c, d). The boundary between the neck and the base is also very distinct. The base of adult and old scales can grow to a considerable height and show a complicated form. The base of scales of more regular (hexagonal) form has the same contours as the crown (Fig. 10a, b, k, l). The base is not extended beyond the crown boundaries, the lateral walls are vertical, or gently convex, and the depression on the lower side is surrounded by low protuberances, sometimes subdivided. The base of polygonal scales, those with more complex contours, can have an odd form (Fig. 10e, j–l). Funnel-shaped deep fissures and protrusions (Fig. 10j–l) are developed on the lower surface. Fissures

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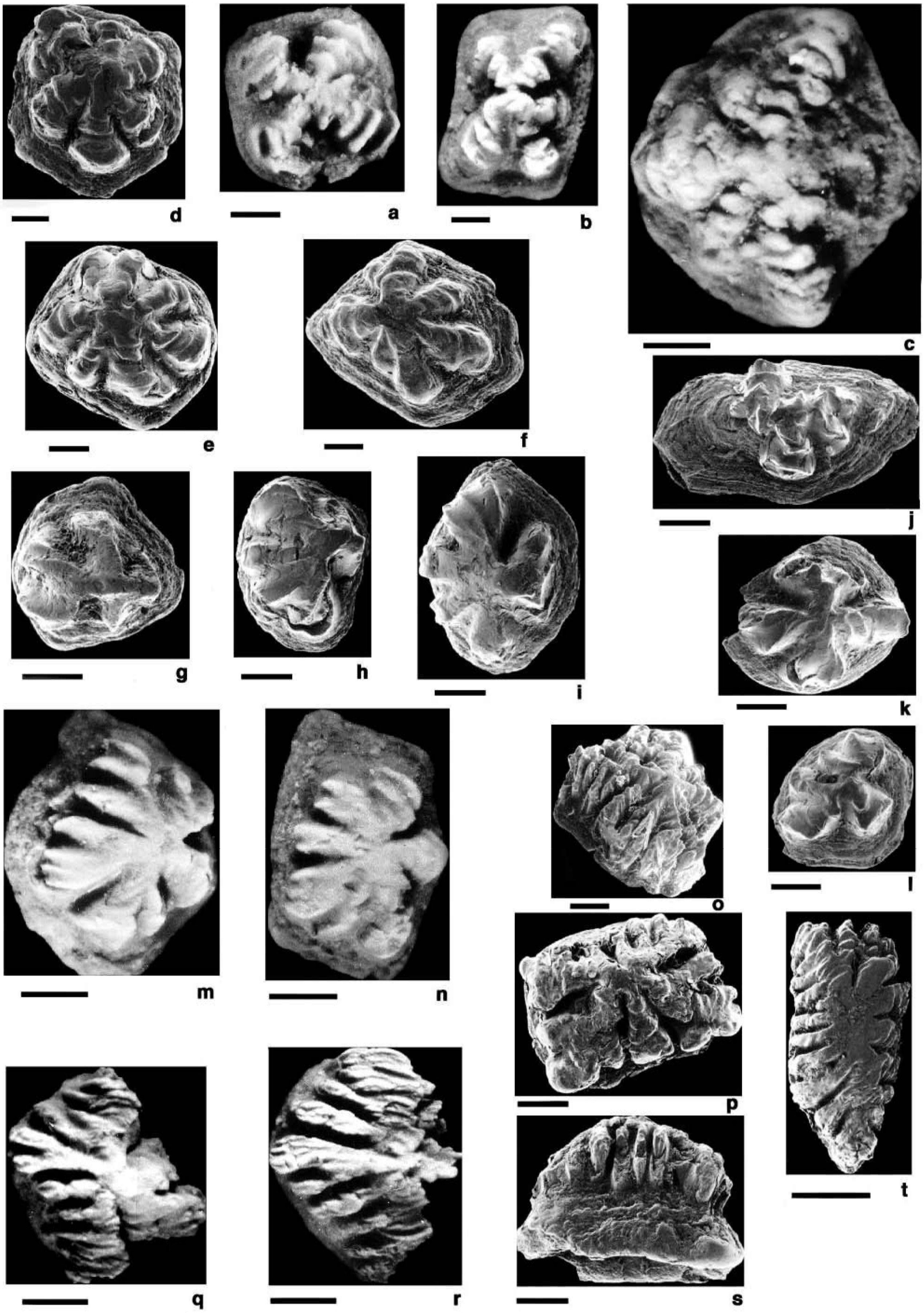

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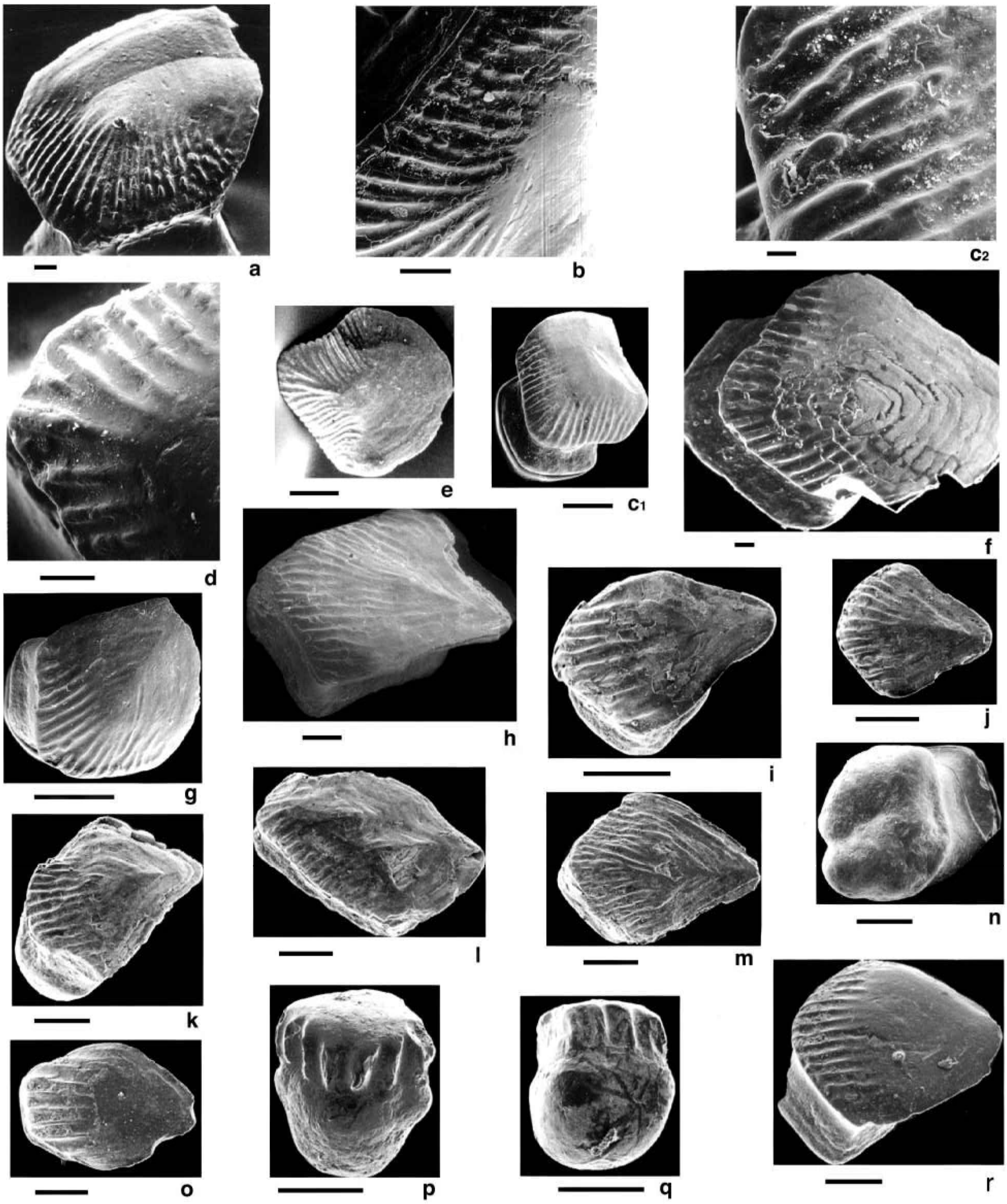

Figure 12 *Tchunacanthus obruchevi* gen. et sp. nov.: (a, c_1, r) body scales with high neck in crown view; (b, c_2, d) enlarged view of body scales showing coronal sculpturing of ridges in anterior part; (e) transitional scale in crown view; (f) body scale with longitudinal ridges on anterior part and concentric, equidistant growth zones posteriorly, in crown view; (g–k) body scales in crown view; (1) body scale, crown view showing two centres of growth; (m) holotype, body scale in crown view, LIG 10-517; (n) body scale in basal view; (o) transitional scale (?) in crown view; (p, q) unusual transitional scales with high base in lateral view. Nos. LIG M-A001, 10-021, 10-025, 10-018, M-A002, M-A003, 10-028, 10-018, 10-511 to 10-519. Coll. 10—Southern Siberia, Irkutsk Subregion V, Balturino District V_2, Tchuna River outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian; Coll. M-A—NW Mongolia, Mt. Tchagartai, Khutsyn-Bulak beds, Upper Llandovery, Lower Silurian (see Figs 1,2). Scale bars $\supset 250\,\mu$m.

Figure 11 *Tchunacanthus obruchevi* gen. et sp. nov.: (a–f) tesserae of morphotype A in crown view; (g–i, l–n) tesserae of morphotype B in crown view; (o–r, t) tesserae of morphotype C in crown view; (s) tesserae of morphotype C in lateral view. LIG 10-109, 10-108, 10-013, 10-520 to 10-528, 10-011, 10-012, 10-014, 10-529, 10-007, 10-005, 10-530, 10-531. Southern Siberia, Irkutsk Subregion V, Balturino district V2, Tchuna River, outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bars $\supset 250\,\mu$m.

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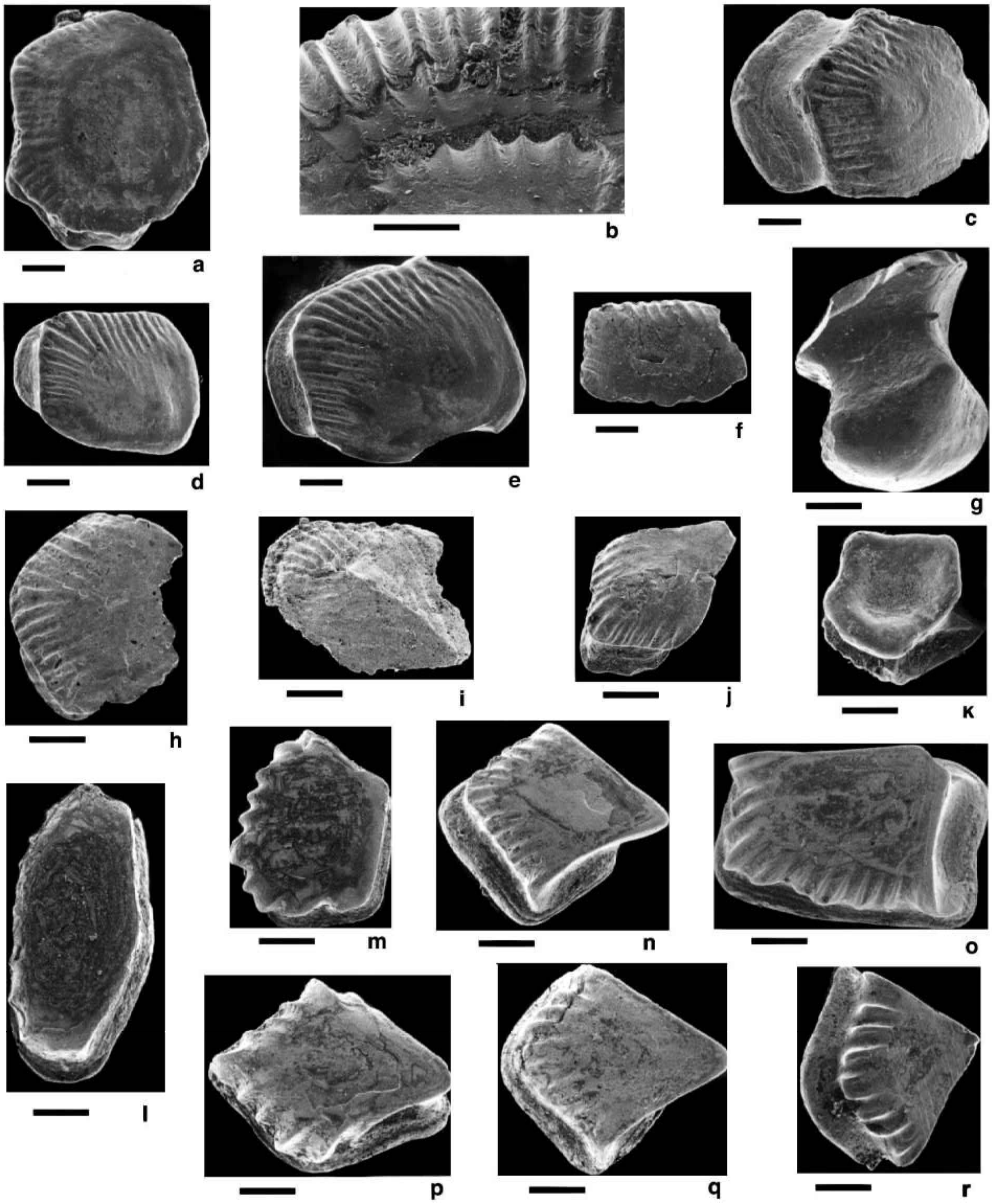

Figure 13 *Tchunacanthus obruchevi* gen. et sp. nov.: (a) polygonal head scale with short ridges in anterior part, crown view; (b) close up of transitional scale with three growth zones clearly demarcated; (c, d, e) body scales in crown view; (g) body scale with high neck in postero-lateral view; (f, h, i, j) body scales in crown view; (k) body scale in basal view. Nos. LIG (a–f) M-A004 to M-A009 (coll. J. Sodov); (g–k) M-A010 to M-A014 (coll. Kh. Rozman); NW Mongolia, Mt. Tchagurtai, Khutsyn-Bulak beds, Upper Llandovery, Lower Silurian. (l–r) *Tchunacanthus* sp.indet.; (1) head scale, widest in transverse axis, crown view; (m, n, o, p, q, r) body scales in crown view. Nos. T-A001 to T-A007; Tuva (Russia), Kyzyl-Tchirzaa Formation, Middle Llandovery, Lower Silurian (see Figs 1, 2). Scale bars $\supset 250\,\mu$m.

extend onto the lateral walls of the base and sometimes onto the crown (Fig. 10c, d).

Tesserae, Morphotype A. (Figs 11a–f; 14a–f). Areal growth is represented distinctly in the crown. The primordial area practically always coincides with the scale centre. The radial arrangement of tuberculate ridges arises from this centre. In Figures 11a and 14c, a small tessera of regular squared shape is represented, with a crown formed of four cruciform radial ridges. Later growth zones increase the width of ridges, and adjacent ridges do not fuse, because the basal area also increases. Ridges are formed of small, low, densely disposed tubercles. An oblong trapeziform tessera is repre-

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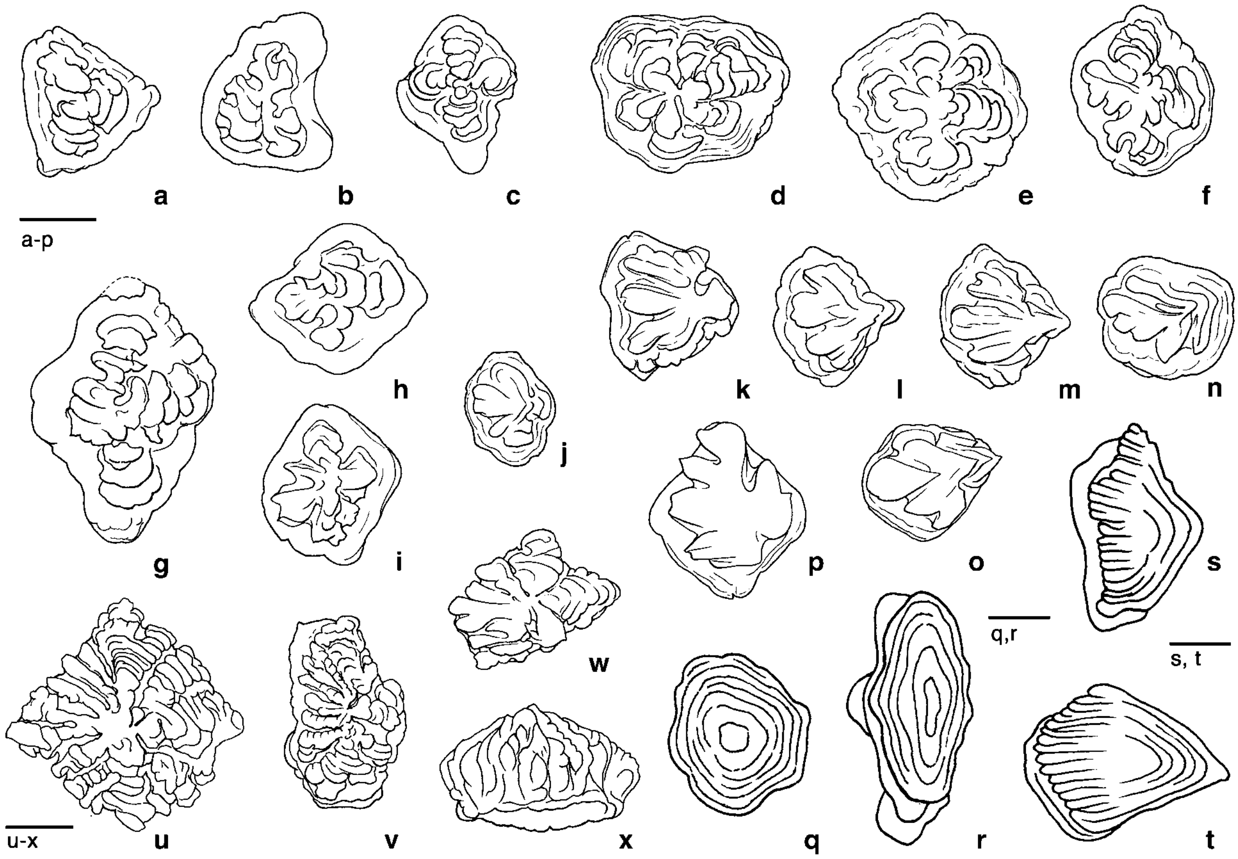

Figure 14 *Tchunacanthus obruchevi* gen. et sp. nov.: morphological set of tesserae and scales: (a–f) tesserae of morphotype A; (g, h) tesserae transitional between morphotypes A and B; (i–p) tesserae of morphotype B; (q, r) head scales; (s) transitional scale; (t) body scale; (u–x) tesserae of morphotype C, (u–w) in crown view, (x) in lateral view. Nos. LIG 10-539 to 10-547; 10-500; 10-503; 10-506; 10-028; 10-006; 10-548 to 10-550. South Siberia, Irkutsk Subregion V, Balturino District V_2, river Tchuna outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bars: a-p $\supset 450\,\mu$m; q, r $\supset 300\,\mu$m; s, t $\supset 200\,\mu$m; u–x $\supset 400\,\mu$m.

sented in Figure 11b, with a crown formed of four complete radial areas and a shorter one. On the crown of large tesserae the number of radial ridges is greater, as many as 7–10, all of unequal length (Figs 11c, d, e; 14d), also the form and disposition of tuberculate ridges varies greatly.

Morphotype B. (Figs 11g–n; 14i–p). Considerable morphological diversity is characteristic of these tesserae. Four paired lobate structures radiate from the centre of the crown. In principle they are bilaterally symmetrical with the growth centre displaced posteriorly. The number of radiating features varies; they are forked in the anterior part, with longitudinal ridges. Most of these tesserae are completely formed with a tall base and a flat or convex bottom. Large tesserae are represented (Fig. 11j) in which the basal laminae would have extended deep into the corium.

Morphotype C. (Figs 11o–t; 14u–x). Crown with a greatly complicated sculpture: two types are found, one isometric, with its primordial area in the centre (Figs 11o, p. s; 14u, x), and the other bilaterally symmetrical, with its crown divided into anterior and posterior sections (Figs 11q, r, t; 14v, w). The latter type has thin, longitudinal ridges with very small tubercles.

Transitional scales. Characteristics of these scales are a relatively short crown, with the anterior surface covered by short, longitudinal ridges and the main part of the surface smooth, with distinct concentric growth lines (Figs 10i; 12e, o–q; 13b; 14s). Growth lines are found on the anterior part of the crown, and they cross the longitudinal ridges (Fig. 13b). Transitional scales have a maximum length of 1.5 mm. There are many smaller scales.

Body scales. These have a typical acanthodian appearance. The diamond-shaped crown is clearly subdivided into anterior and posterior sections. It is larger than the base and projects beyond its boundaries. The anterior edge of the crown is smoothly curved and slightly forward. The posterior part is narrower than the anterior, longer and gently rounded. Some body scales (10%) have more pointed posterior edges and are distinguished by their asymmetry (Figs 12k, 1; 13f). Scales with obvious symmetrical crowns (Figs 12g–j; 13c–e, i,j) are also found.

The crown surface is slightly convex with delicate ridges as sculptural elements in the anterior part where some are formed of tubercles (Fig. 12a–d). The ridges are arranged almost perpendicular to the antero-lateral edges of the crown and are sometimes joined in the medial part (Fig. 12e, h, m). Their length depends on the location, because ridges are quite short on scales of the transitional type and almost reach the centre on typical body scales. Nearer to the centre, ridges become narrower and gradually disappear.

The central and posterior parts of the body scales are smooth, and sometimes have a medial longitudinal crest (Figs 12j–l, 13i). Growth lines are seen on the smooth posterior surface of the crown on most scales (Fig. 12f). The neck is distinct and relatively high on most sculptured scales (Fig. 13c, g). The walls of the neck are entirely smooth (Fig. 13g). Some scales have a low neck and smooth lateral edges (Figs 12h, l; 13i). The base is small (neither large nor high), it is diamond-

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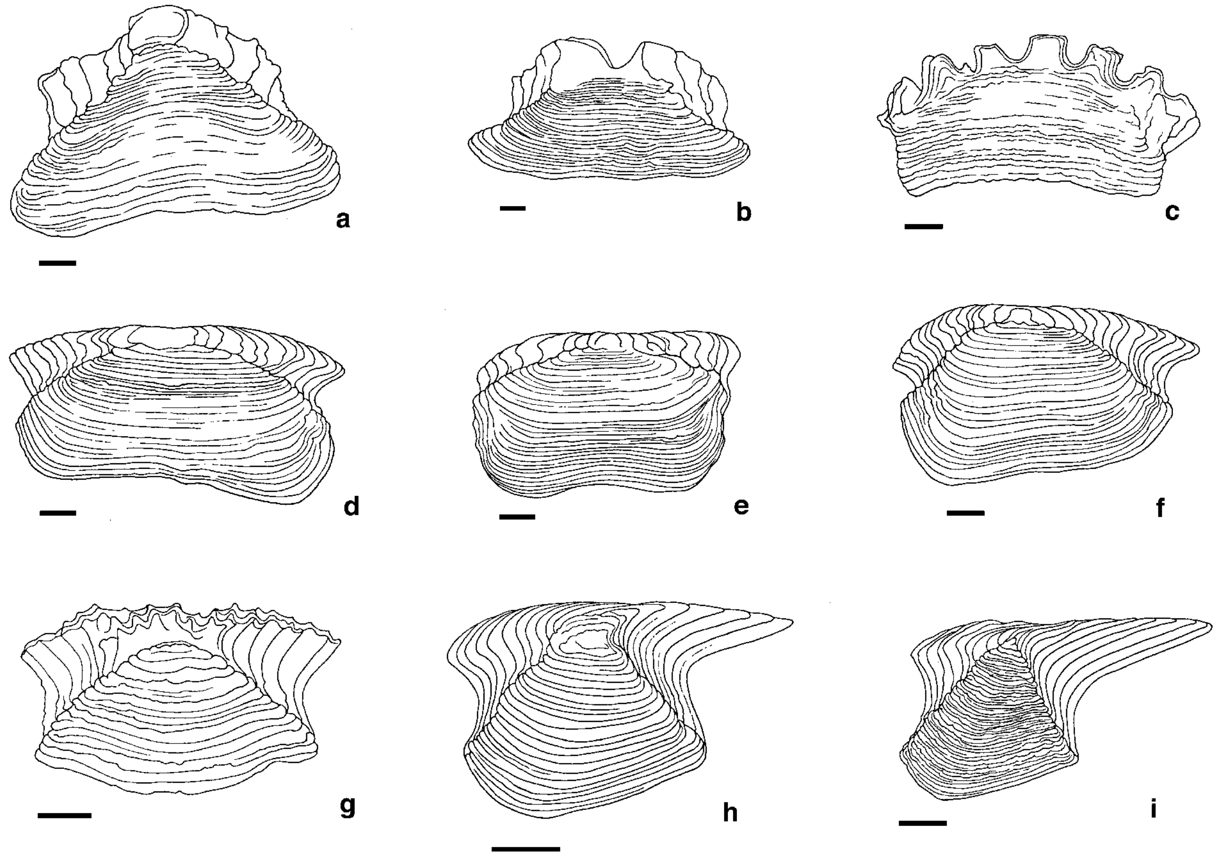


Figure 15 *Tchunacanthus obruchevi* gen. et sp. nov.: growth types of tesserae and scales, from vertical sections, all showing areal growth of base and crown tissue, typical of acanthodians, with layers of crown added independently, after those of base, as size increased. (a) Tessera of morphotype A showing areal growth in crown and base; (b) tessera of morphotye B; (c) tessera of morphotype C; (d, e) head scales; (f) transitional scale; (g) body scale; (h, i) body scales in longitudinal section. LIG 1010, 1020, 1009, 1005, 1004, 1006, 1027, 1026, 1006. South Siberia, Irkutsk Subregion V, Balturino District V_2, Tchuna River outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bars $\supset 100\,\mu$m.

shaped, round, or irregular, and most often slightly convex (Fig. 13g), or depressed in the centre (Figs 12n; 13k).

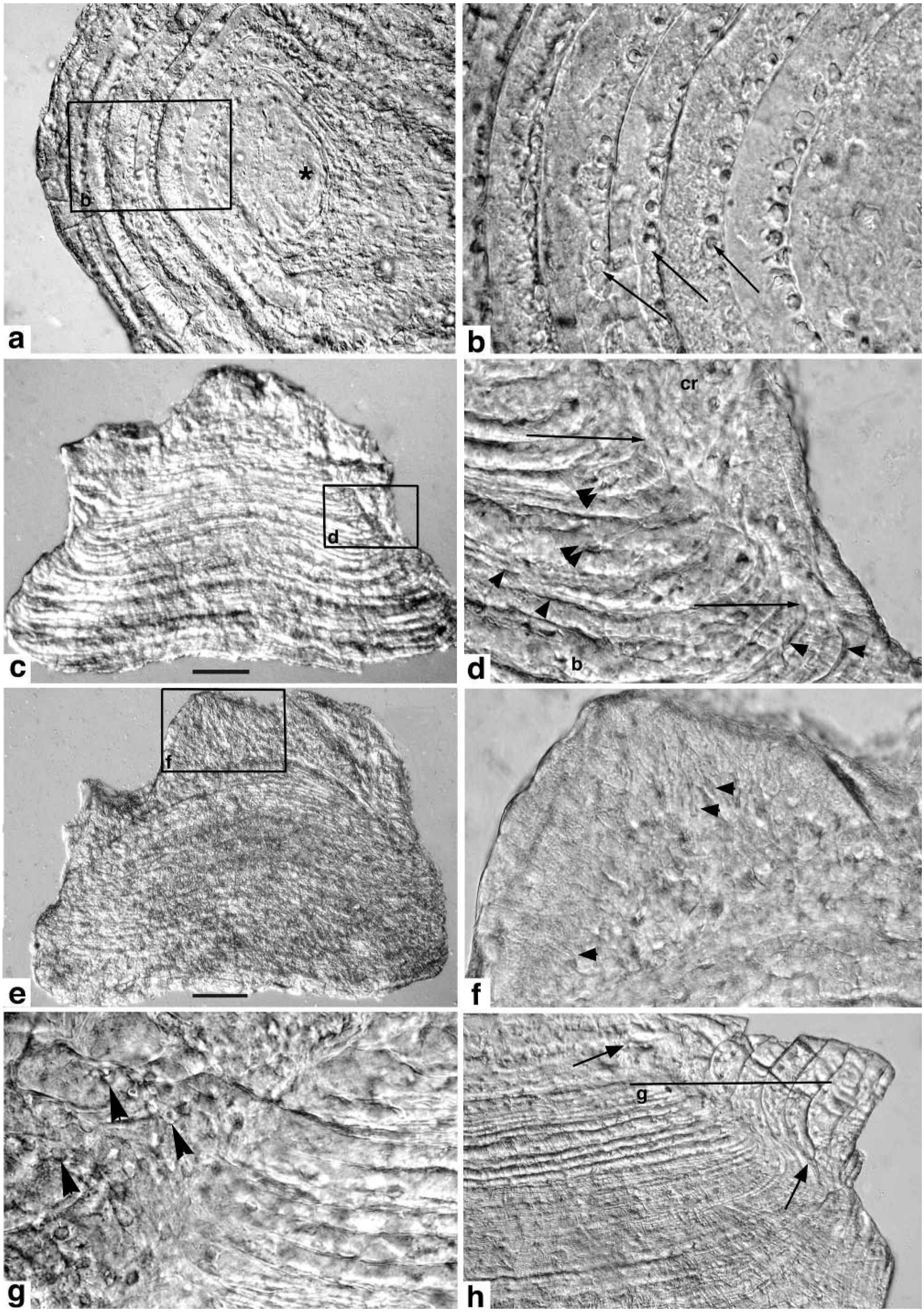
Growth of the scales. In the crown of head and transitional scales, the extent of areal growth can be determined from concentric lines on the surface of the crown. The growth sequence can be traced even more clearly by using both vertical and horizontal sections (Figs 15, 18, 19): consecutive areal growth zones occurred around the primordial (primary) scale laterally and deep onto the base of head and transitional scales (Figs 15d–f; 18a, b). This occurred simultaneously in the crown and the base, each lamina in the base corresponding to each growth layer in the crown. Growth of the crown had sometimes ceased before that of the basal tissue. Areal growth of basal zones of the scales may have been important for greater surface area in attachment to support function in the squamation.

Superpositional growth first occurs on the earliest formed surface of the crown, and each successive layer partly overlaps the former growth area (Figs 15g–i; 19). Such areal-superpositional type of crown growth is noted on a number of the body scales, but partial superpositional growth occurs anteriorly (Figs 15g–i; 19a). Only a few body scales show complete superpositional growth. The later growth areas of most body scales do not overlap the whole surface of the crown. The laminae of superpositional growth are very thin, two to three times thinner than on lateral areas, in the central part of the crown.

In morphotypes of tesserae A, B and C, the growth lines in the basal tissue of the first sequence are horizontal in the upper part, then down-turned peripherally; they only turn upwards in the most basal layers. Basal layers can be added after crown growth has stopped (Fig. 15a–c, g, h).

Histology. The crown of scales of all morphological varieties is formed of a very dense dentine tissue, which is called cellular mesodentine. (The widespread use of the term 'mesodentine' for all dentine types not obviously orthodentine or semidentine, requires a distinction between mesodentine with cell body

Figure 16 *Tchunacanthus obruchevi* gen. et sp. nov.: photomicrographs of thin sections: (a, b) body scale, horizontal section showing central primordial part (asterisk) and area in inset (b) high magnification, odontocyte lacunae proximal in each layer (arrows), LIG 1022. (c, d) tessera of morphotype A in vertical section (see Fig. 15 h, i) with high magnification (inset in d) of the junction (arrows) between crown layers (cr) and base (b), where growth layers are prominent (arrow heads), LIG 1010; (e, f) tessera of morphotype B, vertical, longitudinal section with area of higher magnification (inset f) to show the distal polarity of the branching tubuli of the odontocyte lacunae (arrow heads) in the mesodentine of the crown, LIG 1329; (g, h) head scale, left side in vertical section (odontocytes arrow heads in g), (h) right side with clear areal growth zones in both the crown and the base, junction is arrowed, the line 'g' is the equivalent position of the higher magnification of the left side shown in (g), where cells of the mesodentine are clear in each layer of the crown. Scale bars c, e $\supset 100\,\mu$m.



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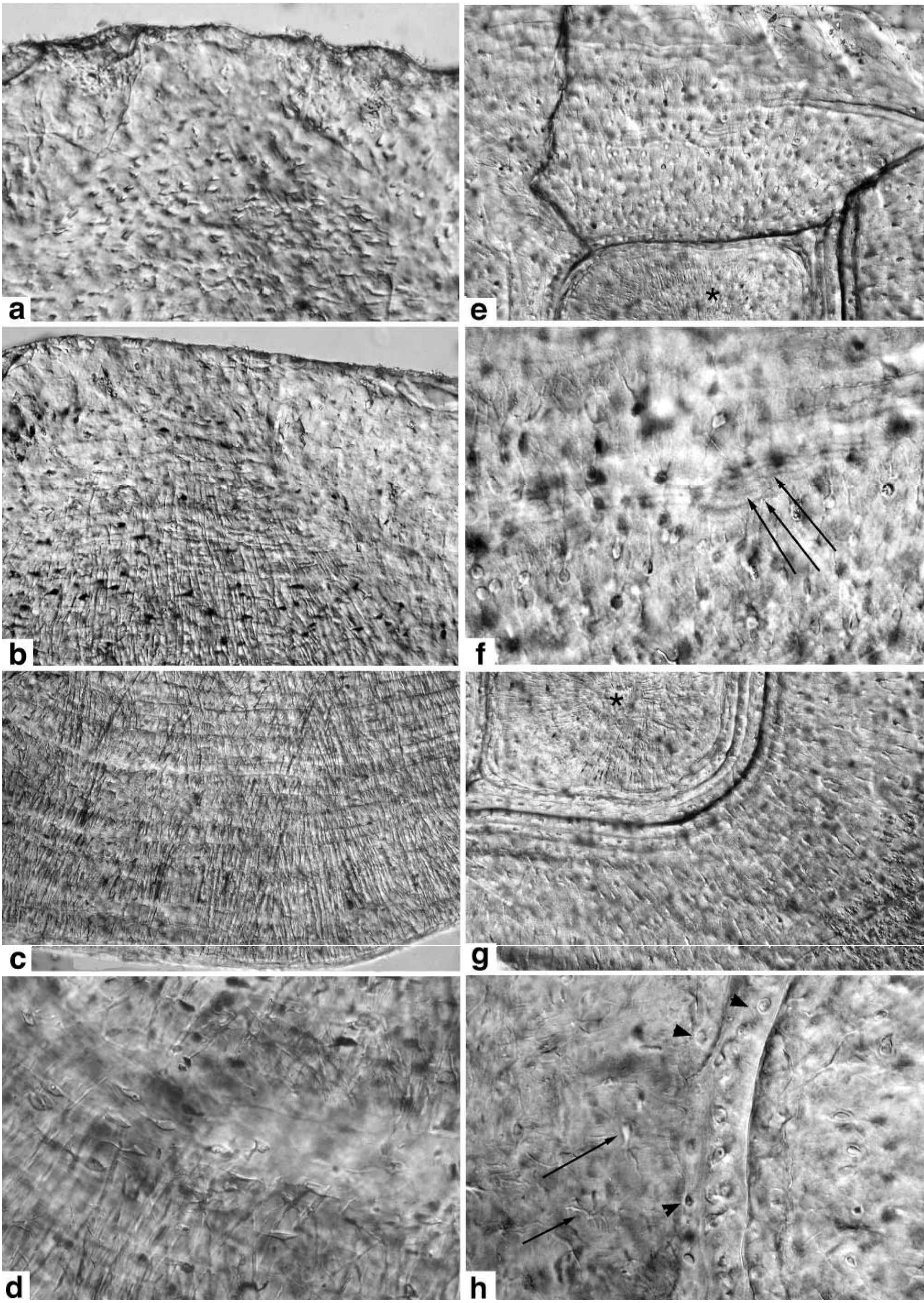
a
b
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*

spaces, and that without enclosed cell bodies; both have a reticular network of cell process spaces, seen as branching tubuli.) Only one row of small cell spaces is present in each dentine layer in a proximal position (Figs 16a, b, g, h; 17g, h). Both short and long, thin tubules project distally from each cell space (Fig. 16f). This arrangement of separate cell spaces is clearest in horizontal sections (Figs 16a, b; 17e–h), where the unipolar cells with one, or two to three dentine tubules are shown. A system of horizontal and ascending canals, characteristic of scales of later acanthodians, is not present.

The base of all scales is a dense lamellar tissue with numerous alternating fibre bundles (Fig. 17c, d) whose radial arrangement, normal to the basal surface, is best seen in polarised light. Simple, irregular cell spaces are more numerous in the upper part of the base (Fig. 17a), but all are disposed parallel to the growth lines and are more fusiform in the lower layers (Figs 17b, d). Junctions between each growth zone of the first sequence are very distinct on both the crown and the base; also, thin growth laminae of the second sequence in the crown are seen within each of the first zones (Fig. 17f). Essentially, each zone in the crown matches each growth lamina in the base. It is obvious in all morphological types (Fig. 15). The growth layers of head scales with complex high bases are reflected upwards only peripherally; in the central part they are horizontal. The unmineralised cavities, formed in the regions where Sharpey's fibres attach the base to the corium, are seen as thin tubular spaces and are disposed perpendicular to growth lines (Fig. 17b–d).

Comparison. Atypical scales of *T. obruchevi* were discovered in the upper part of the Staroe Balturino outcrop (outcrop 135, beds 63, 64, Barmo Formation, Lower Wenlockian). The areal growth of the crown in body scales and in some transitional scales is not so sharply expressed and superpositional growth prevails. Head scales are seldom found. Some body scales with crown structure characteristic of *T. obruchevi* were discovered in Upper Llandoverian deposits of the Turukhansk District (Yassenga area, borehole Yass-4, depth 1059.7 m). Limited material has not permitted examination of sections and so their inner structure is unknown.

More than 200 head, transitional and body scales identical to *Tchunacanthus obruchevi* scales from the type locality near the village of Staroe Balturino in the Irkutsk amphitheatre are found in the samples from northwestern Mongolia. No tesserae have been found among them. Rather than putting tesserae and anomalous scale types into another species, we have included them in *T. obruchevi* because of their similar growth patterns and histology. A similar difficulty exists in determining the limits of topographical variability in the squamation of *Nostolepis striata* Pander. The tessera-shaped scales of that species were attributed by W. Gross to a special species, *Nostolepis robusta* Gross (Gross 1971).

Observations. There is no doubt that a large area of the body was covered by tightly joined scales, with smooth crowns, including the anteriormost part of the squamation of *Tchunacanthus obruchevi*. As determined by the extent of scale growth, the bases were set deeply in the corium and grew more in depth than in width. It may be supposed that lateral-line canals could be housed in the basal furrows, and that the vertical furrows on the lateral margins of the crown would link these via vertical canals to pores at the surface (Fig. 10c, d). A similar system of lateral-line canals and vertical pores, located among closely adjoined scales, is found on head scales of thelodonts belonging to the Turiniida (see Karatajute-Talimaa 1978, pl. XLI, figs 1, 2).

Geological and geographical range. Lower Silurian, Upper Llandovery, Upper Balturino Subformation of the Balturino District, outcrop 135, beds 43–62 (Tchuna River, near the village of Staroe Balturino), outcrop at Parenda creek (Tchuna River basin); upper part of Rassokha Formation on the Ilim District (station Tushama, outcrop 141, beds 39–48); Upper Llandovery of the Turukhansk District (borehole Yassenga-4, depth 1059·7 m); Upper Llandovery, Khutsyn-Bulak Beds of northwestern Mongolia (district of the Tchagartai mountain ridge, see Figs 1, 2).

Material. About 10,000 well-preserved scales are in the collection from the type locality (outcrop 135, Staroe Balturino). Colour of scales is light-yellow, almost white, brownish-yellow. About 200 brown-coloured, well-preserved scales are in the collection from northwestern Mongolia. All material has good histological preservation.

Tchunacanthus sp.indet.
Figure 13l–u

Material. About 30 well-preserved scales have been discovered in Middle (Upper?) Llandoverian deposits of Tuva (Kyzyl-Tchizaa Formation). These have the same inner structure as scales of *Tchunacanthus obruchevi* fron Siberia and northwestern Mongolia, but differ in morphological features.

Head scales have areal growth in the crowns with short ribs on the anterior margin (Fig. 13l). Transitional scales have a short posterior part of the crown and distinct crenulation in the antero-lateral parts (Fig. 13m). Body scales (Fig. 13n–u) have short, distinct, but not numerous ridges on the antero-lateral surface of the crown, and some are asymmetrical (Fig. 13o). The posterior part of the crown can be short (Fig. 13o, p), or elongated (Fig. 13n, q, u). The neck of all morphological types of scale is distinct, but not very high, with a smooth surface.

4. Discussion

4.1. Morphology and location on the body

In some interbeds of sandstone of the Upper Balturino Subformation, the vertebrate microremains form accumulations resembling a 'bone-bed'. The main mass of these remains belongs to *Tchunacanthus obruchevi*. The great numbers and morphological diversity of scales, tesserae and plates presents the possibility of compiling a 'morphological set', as a reliable

Figure 17 *Tchunacanthus obruchevi* gen. et sp. nov.: photomicrographs of thin sections. (a–d) Body scale in vertical section to show tissue detail from crown to base, where osteocyte lacunae are very obvious and numerous in upper part, apex of base, (a, b), also Sharpey's fibres are very abundant in all regions, including apical part of base (b); both osteocyte lacunae and spaces from the Sharpey's fibre bundles are seen at high magnification in (d); (c) basal region with alternating direction of the Sharpey's fibres and lines from concentric areal growth; (a) LIG 1350; (b–d) LIG 1327. (e–h) Horizontal sections of body scale to show tissue details of cellular mesodentine, cell processes are especially clear in each dentine layer, with distal polarity; (e, g) are medium magnification of two adjacent regions around the central part of the scale (asterisk); (f, h) are high magnification from each field. In (e, f) closely spaced lines due to incremental growth are seen within one layer (arrows); (g, h) junction between the basal tissue, osteocytes (arrows), and first layer of coronal dentine with distinct odontocyte lacunae (arrow heads); LIG 1190. NW Mongolia, Mt. Tchagartai, Khutsyn-Bulak beds, Upper Llandovery, Lower Silurian.

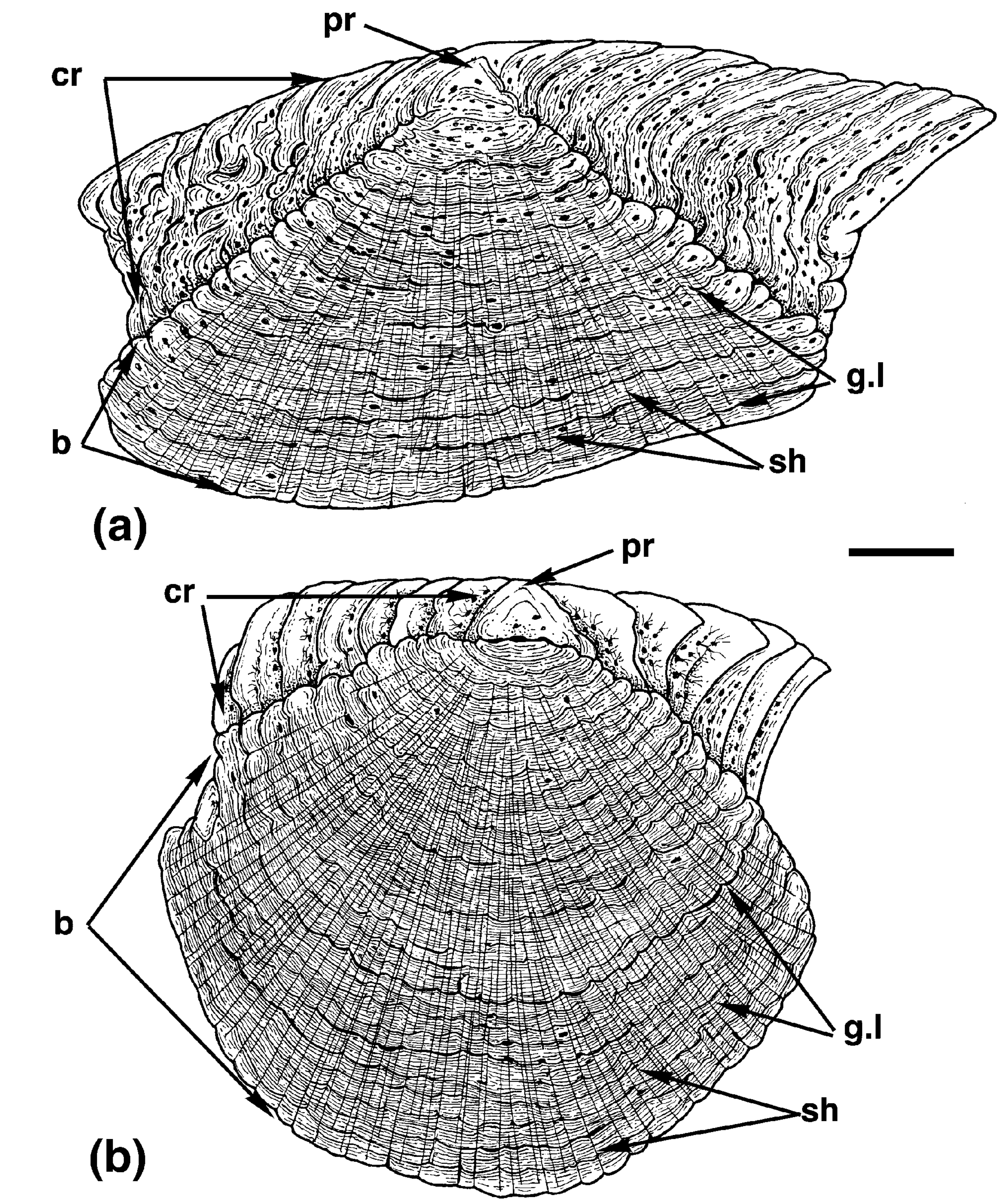

Figure 18 *Tchunacanthus obruchevi* gen. et sp. nov.: generalised representative drawings of the histology from vertical, longitudinal sections through (a) transitional scale LIG 1013; (b) a rare large based scale LIG 1333; Southern Siberia, Irkutsk Subregion V_1, Balturino District V_2, Tchuna River, outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bar ⊃ 100 μm. Abbreviations: b—base; cr—crown; g. 1—growth lines; gl. d—globular dentine; pr—primordial scale; sh—Sharpey's fibers; x—folds in the dentine layers.

representation of the squamation of this new genus and species of acanthodian. These are united on the basis of identical structure, tissue types, patterns of growth, and relative distribution of these in the crown and the base. It is proposed that within the morphological set body locations can be assigned to the different shapes, and that tesserae as well as scales will be found on both the head and the trunk. These tesserae are described as morphotypes 'A', 'B' and 'C', and others as head scales, transitional scales and body scales.

The tesserae of morphotype 'C' are very specific, as they have a complex crown and concave visceral surface to the basal plate. This morphology suggests that these scales were

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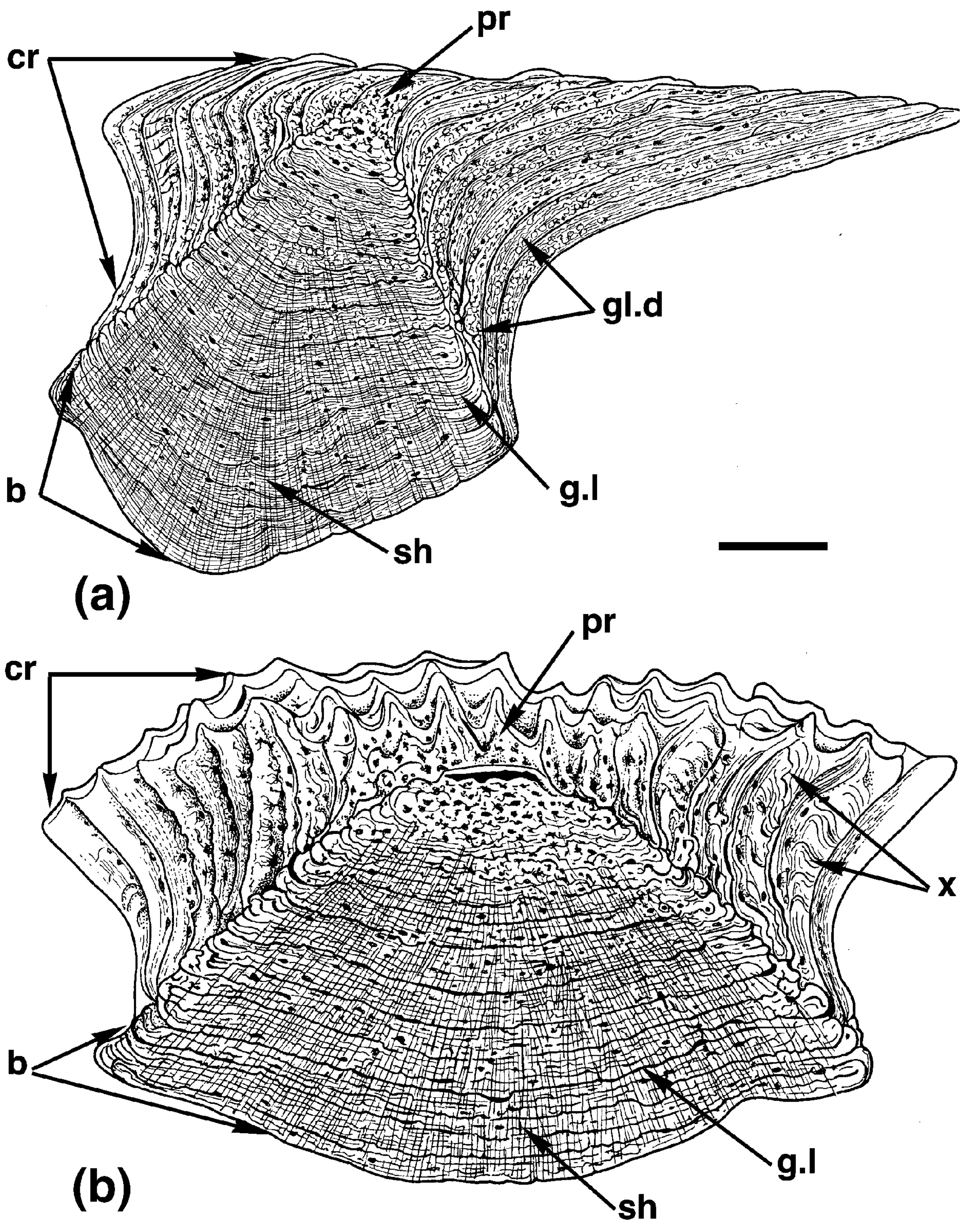

Figure 19 *Tchunacanthus obruchevi* gen. et sp. nov.: generalised representative drawings of the histology from (a) vertical longitudinal section through body scale LIG 1102; (b) vertical transverse section in the anterior part of body scale LIG 1127. Southern Siberia, Irkutsk Subregion V_1, Balturino District V_2, Tchuna River, outcrop 135, beds 43–49; Upper Balturino Subformation, Upper Llandovery, Lower Silurian (see Figs 1, 2). Scale bar $\supset 100\,\mu$m. Abbreviations: b—base; cr—crown; g. l—growth lines; gl. d—globular dentine; pr—primordial scale; sh—Sharpey's fibers; x—folds in the dentine layers.

from a specific site within the exocranium. These could not be disposed along the ventral part of the body, as analogues of the 'paired post-pectoral fin fold spines' (Ørvig 1967, textfig. 2; plate 1, figs 3, 40), because they have well-developed, anterior and posterior portions to the crown (Figs 11q, r; 14v, w). Certainly, the few with more spiniform crowns together with very small and exaggerated concave bases (Figs 11s; 14x) could be rudimentary fin spines, as a pre-adaptation for spines. Despite this large collection of various morphologies, true fin spines are not represented in the Tchunacanthidae (see comments on the material in section 2).

Until more fossils with articulated squamations are found, the disposition and succession of scales and tesserae in the tchunacanthids can only be speculated upon. However, analogy is possible with a similar 'morphological set' of *Nostolepis striata* Pander. Gross (1971) established a generalised set for the dermal skeleton of this species from his studies of abundant microremains from the Upper Silurian (Ohesaare, and boulders from the Lowland of N Germany). In addition to simple scales on the trunk and tail, the other types show three kinds of sculpture: (i) coronate tubercles on tesserae; (ii) stellate tubercles on scales and tesserae; (iii) pearl-shaped tubercles on scales and tesserae. Gross also suggested that polygonal plates (tesserae) were part of the exocranium on the dorsal surface, as well as transitional forms of scale between these tesserae, at the boundary between head and trunk.

The dermal skeleton of representatives of the Tchunacanthida described here, from both sites, differs considerably from that of the Climatiida as described by Gross (1971), in particular because no examples of teeth or fin spines have been found. However, by comparison of *Tchunacanthus obruchevi* with *Nostolepis striata* we have noted significant differences:

(1) Head scales with areal growth in the crown are confined to *T. obruchevi*.
(2) The crown of transitional scales shows little superpositional growth and they already resemble body forms with a short posterior section of the crown.
(3) In body scales, superpositional growth is expressed in the anterior part, while in the posterior part growth is areal.
(4) The primordial element of the crown is superficial within the superpositional layers of the crown, and not deeply buried as in *N. striata*.

Dension (1979, p.5, fig.4B) considered the amount and extent of dermal bone present in the exocranium of the various families of acanthodian. In most representatives, the circumorbital bones were well developed, with those of the Climatiidae particularly thick and well ornamented. The cranial roof and cheeks of many climatiids were covered by many diverse forms of bones with great size variation, described as polygonal plate-tesserae and scale-tesserae.

The relatively heavily armoured condition of the climatiids is considered as both primitive and specialised states, depending on the opinion of the authors. However, we have described scattered skeletal elements of one of the earliest acanthodians known so far and note that in this genus, *Tchunacanthus*, very solid dermal armour is present. If this is presumed to be a primitive species, it confirms that a heavily armoured condition is present, at least early in the evolution of the group. It would be of great value to use the characters of the body armour, determined only from disarticulated microremains, together with whole body characters in a cladistic analysis to determine polarity of the skeletal states in the body armour.

4.2. Histology

We have described and illustrated a very specific form of mesodentine in the Tchunacanthidae, with cell body spaces included in each layer of dentine (see section 3). It differs from types of mesodentine, as illustrated in some thelodonts (Karatajute-Talimaa 1978, pls 5, 6, 8, 10, 12 and 13), where tubules branch distally from thick tubular spaces, the pulp canals. It is also different from the mesodentine of a primitive, presumed chondrichthyan, *Elegestolepis grossi* from the Upper Silurian of Tuva (Karatajute-Talimaa 1973, figs 4D, 5), a type with a central pulp cavity. Of the vertebrates occurring in the Ordovician, one is remarkable for the presence of cell body spaces in the dentine, *Skiichthys halsteadi* Smith & Sansom from the Harding Sandstone of North America (Smith & Sansom 1997). Smith & Sansom (1997) discussed the likely affinities with acanthodians and other early vertebrates. The tissue of the crown was referred to as mesodentine (because of the included cell spaces). Together with the osteocytic basal bone of the denticle, this was regarded as evidence of the primitive occurrence of cellular skeletal tissue co-occuring in dentine and bone at the same stage of evolution (Smith 1991). The conclusion was that neither gave rise to the other, and also that cellularity gave rise to acellularity in many evolving lines of early vertebrates. Tissue of the new acanthodian from the Lower Silurian (Siberian platform) described here, also demonstrates this trend, as later forms of acanthodians have branching tubules but no cell body spaces in the dentine. Smith & Sansom (2000) have commented, in a review of all early dentine types, that mesodentine is not a transitional form between bone and dentine. We suggest here that in the future new terms should be used and evaluated for all further descriptions, such as odontocytic (cellular) dentine and syncitial dentine, for a joined network of branching tubules without cell spaces. The latter type is illustrated by Gross (1947, 1973) in *Nostolepis striata* and *Acathodes bronni*; both are acanthodians from the Lower Devonian and arguably more derived types of scale. The histology of scales of the Lower Devonian *Poracanthodes* (Valiukevičius 1992) also looks quite different, with strong branching tubules and no cell lacunae, and also with a radial system of pore canals. Some of the figures of *Nostolepis* (Gross 1971, figs 17M, 18A–E) show irregular-shaped lacunae, or slender, fusiform lacunae, in the dentine layers of the crown tissue, but these scales also have vascular canals in the crown, not seen in the acanthodians described here, *Tchunacanthus* and *Lenacanthus*. With growth from the outermost surfaces being the predominant mode, nutrients can be supplied from this route during growth, without the need for vascular canals within the tissues. General levels of ion composition and tissue fluid can be maintained and regulated by the enclosed cells, if these tissues are compared with cellular bone and the role of osteocytes, whose accepted function is that of calcium homeostasis.

The basal tissue is a cellular bone with a dense distribution of radial fibre bundles for attachment, and slender cell lacunae variously distributed, sparse in the lower layers and numerous in the first-formed coronal part below the crown tissue. Again, the basal tissue of *Skiichthys* (Smith & Sansom 1997) is similar in these two features but is lacking the more obvious growth layers as typical of acanthodians. It is noteworthy that there are thin tubule spaces aligned with the direction of the fibre bundles. These are presumed to remain from the unmineralised core of collagen after dissolution in the fossilisation process. However, it is beyond the scope of this paper to evaluate any alternative reasons for tubule spaces, such as cell process spaces from the fibroblasts, as this requires a more comparative approach amongst other types of scale and their likely attachment to the corium.

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