PHYLOGENIE UND EVOLUTIONSÖKOLOGIE DER HEXACTINELLIDA (PORIFERA) IM PALÄOZOIKUM

Dorte Mehl

Mit 15 Abbildungen und 7 Fototafeln

Zusammenfassung:
Die Hexactinellida, erstmals aus dem Jungproterozoikum von China nachgewiesen, sind die ältesten Tiere der Erdgeschichte, die einer heute noch lebenden Metazoengruppe eindeutig zuordenbar sind. Bereits im Mittelkambrium zeigen die Hexactinellida eine bemerkenswert hohe Diversität. Neben vielen ausgestorbenen Gruppen, wie z.B. die Protospongiidae, sind die Hauptgruppen der rezenten Hexactinellida, die Schwestergruppen Hexasterophora und Amphidiscophora, bereits seit Frühpaläozoikum bekannt. Die paläozoischen Großtaxa, Reticulosa und Brachiospongiidae, führten möglicherweise zu den rezenten Hexasterophora und Amphidiscophora. Erste Vertreter der Hexactinosa, die vor allem innerhalb der mesozoischen Spongiolithe eine wichtige Rolle spielten und auch in rezenten tiefmarinen Environments weite Verbreitung zeigen, sind seit dem Devon bekannt. Eine wahrscheinlich paraphyletische Gruppierung, die anscheinend vorwiegend auf Tiefwasserhabitate beschränkten „Rossellimorpha", ist in ihrer Skelettarchitektur seit dem frühen Kambrium konservativ geblieben. Zu manchen Zeiten der Erdgeschichte konnten jedoch spezialisierte Gruppen der Reticulosa, z.B. die Dictyospongiidae, die Fähigkeit entwickeln, unter flachmarinen, höherenergetischen Bedingungen zu leben. Im späten Paläozoikum, insbesondere während des Perms, fand innerhalb der Hexactinellida eine hochdiverse Entwicklung verschiedener Skelettypen statt, unter anderem „Lithistiden"-ähnliche Gerüste mit Zygose und auch Formen mit demospongioiden Nadelzügen. Der wichtigste Faunenschnitt in der Geschichte der Hexactinellida fand am Ende des Perms statt. Es gibt jedoch keinen Hinweis auf ein größeres Aussterbe-Ereignis an der Frasne/Famenne-Grenze. Die räumliche/stratigraphische Verteilung der Spongien und Vergesellschaftungen isolierter Spicula, insbesondere innerhalb frühpaläozoischer Sedimente, geben wichtige palökologische Hinweise. Eine evolutionsökologische Auswertung der Organismengruppen erweitert die palökologische Methode. Der Wert dieses Konzepts, beispiesweise für das Verständnis taphonomischer und sedimentärer Vorgänge, wird anhand einiger Beispiele der paläozoischen Porifera gezeigt.

Abstract:
The Hexactinellida, first appearing in the Late Proterozoic of China, are the earliest animals in Earth's history, which can be definitely attributed to an extant metazoan group. Already in the Middle Cambrian the hexactinellids show remarkably high diversity. Beside many specialized extinct groups, such as the Protospongiidae, the main groups of the recent Hexactinellida, the sister groups Amphidiscophora and Hexasterophora, are known since the Early Paleozoic. The large Paleozoic taxa, Reticulosa and Brachiospongiidae, known since the Cambrian and Ordovician, respectively, may have given rise to the recent Hexasterophora and Amphidiscophora. First representatives of the Hexactinosa, important sponges of the widely distributed Mesozoic spongiolithic facies and common also in recent deep sea environments, are known since the Devonian. A probably paraphyletic grouping, the "Rossellimorpha", stayed conservative in its skeletal achitecture from the Early Cambrian until today, most of the time apparently restricted to deep-sea habitats, similar to those of most recent hexactinellids. During some periods of Earth's history, specialized groups of the Reticulosa, e.g. the Dictyospongiidae, developed the ability to live in shallow water under higher-energetic conditions. The Late Paleozoic, especially Permian, was a time of highly diversified spicular skeletal types within the Hexactinellida, including "lithistid"-like frameworks with zygosis and also groups with demospongioid spicule tracts. During the history of the Hexactinellida, the main faunal extinction occurred at the end of the Permian. However, no major extinction event is recorded at the Frasnian/Famennian boundary. The distribution of sponges and assemblages of isolated sponge spicules, especially for Early Paleozoic sediments, gives important palecological indications. An evolutionary-ecological evaluation of organismic groups expands the method of palecology. The value of this concept for our understanding of e.g. taphonomic and sedimentary processes is demonstrated by some examples on account of paleozoic Porifera.

1. Methodik

Die Probleme der Erforschung paläozoischer Kieselschwämme stellen sich grundsätzlich anderes als bei den mesozoischen. Zum einen ist die fossile Überlieferung nur sporadisch und beschränkt sich auf sogenannte „Fossilisations-Fenster". Gerade in Europa sind die aufgeschlossenen Vorkommen, verglichen mit den ausgedehnten spongiolithischen Serien des Juras und den „Schwammrasen" der Spätkreide, eher ärmlich. Zum anderen ist für die altertümlichen Hexactinelliden das Prinzip der Aktuopaläontologie nicht in dem Maße anwendbar, wie es für die mesozoischen praktiziert wurde (MEHL, 1992). Die mesozoischen Hexactinellida, insbesondere die spätkretazischen, lassen sich relativ problemlos in die rezent-taxonomische Systematik dieser Gruppe eingliedern. Bei den prätriassischen Taxa handelt es sich dagegen überwiegend um ausgestorbene Gruppen, die sowohl in ihrer Morphologie als auch in palökologischer Hinsicht von den heutigen Hexactinelliden zum Teil wenig gemein haben.

Abweichungen vom Paradigma der streng abwärts systematisierenden Taxonomie (AX, 1989; u.a.), waren aus diesen Gründen unerläßlich. Das von MEHL (1992) vorgeschlagene Konzept des **cladogenetischen Chronogramms** versucht eine Synthese zweier konkurrierender methodischer Ansätze in der biologischen Klassifikation zu erreichen: Einerseits die traditionell paläontologische, aufwärts klassifizierende Methode und andererseits das streng hierarchisch kladistische, zeitlich nicht dimensionierte taxonomische Argumentationsschema. Das cladogenetische Chronogramm beruht auf der phylogenetisch-systematischen Merkmalsanalyse nach HENNIG (1950, 1966), jedoch spielen auch paläontologische Argumente wie das paläogeographisch-zeitliche Auftreten der Merkmalskomplexe eine entscheidende Rolle. Das HENNIGsche Argumentationsschema bildet auch in dieser Arbeit die Grundlage der Ausgangshypothese, jedoch liegt der Schwerpunkt der weiteren Analyse auf dem stratigraphischen, paläogeographischen und palökologischen Auftreten der jeweiligen Gruppenmerkmale (Autapomorphien). Aus diesen Daten lassen sich bei ständiger Kontrolle durch den Außengruppenvergleich Schlüsselfragen der Evolution, z.B. die Homoplasie-Wahrscheinlichkeit eines Merkmals, beantworten.

1.1 Das Konzept der Evolutionsökologie

Die Evolutionsökologie ist die Wissenschaft der Erschaffung ökologischer Nischen im Zuge der Speziation und der Erschließung ökologischer Zonen durch phylogenetische Radiation. Sie befaßt sich zugleich mit Fragen der Anagenese, der Adaptation und der Koevolution (v. WAHLERT, 1978). In der Paläontologie ist sie die Methode, anhand von Fossilien möglichst genaue palökologische, paläogeographische und taphonomisch-sedimentologische Aussagen zu erlangen. Derzeit arbeitet die Autorin an der Ausarbeitung einer konkreten evolutionsökologischen Methodik, die zur breiten Anwendung dieses Konzeptes für alle Organismengruppen anregen soll. Die von einigen Paläontologen (z.B. NIELSEN, 1992; u.a.) eingesetzte **Ökostratigraphie** arbeitet in eine ähnliche Richtung, nur ist die Evolutionsökologie noch stärker paläobiologisch und phylogenetisch-systematisch ausgerichtet. Diese beiden Konzepte können einander hervorragend ergänzen, und ihre Synthese wird vielleicht die paläontologische Antwort auf die Sequenzstratigraphie, in der vielfach versucht wird, ohne Rücksicht auf die Bioevolution eine Stratigraphie zu erstellen. Die Ökostratigraphie ist eine Alternative zur Sequenzstratigraphie, insbesondere für kondensierte und flachmarine Schichtenfolgen. Mit Hilfe einer kombinierten Methodik der Evolutionsökologie/ Ökostratigraphie lassen sich charakteristische Environment-Parameter, wie z.B. Sedimentationsmechanismen, Paläoströmungen und -bathymetrie erschließen. Es geht darum, für jede Organismengruppe die spezifischen aut- und synökologischen Ansprüche zu jedem gegebenen Zeitpunkt der Erdgeschichte festzulegen. Ein Abriß dieser Methodik soll den Blickwinkel und das Vorgehen der Autorin verdeutlichen.

Obwohl das Wort „Evolutionsökologie" in der zoologischen Literatur immer wieder verwendet wird, ist es ist mir bisher nicht gelungen, eine konkrete Definition zu finden. Folgende Umgrenzung dieses Begriffs wird deshalb vorgeschlagen:

Evolutionsökologie:
Die ökologisch-phylogenetische Koppelung – Erschließung ökologischer Zonen und Nischen im Zuge der Speziation – und ihre Entwicklung in Zeit und Raum.

Theoretische Voraussetzungen:
1. Eine phylogenetische Systematik (HENNIG, 1950, 1966).
2. Ein dynamisches Nischenkonzept (GÜNTHER, 1950).
3. Die Verknüpfung der Entwicklung ökologischer Zonen mit der Phylogenese einer Gruppe: „Artenspaltung heißt Nischentrennung" (SCHMITT, 1982, 1985).

Kurzformel zur Erarbeitung der Evolutionsökologie einer Gruppe (B.E.H.):
Biologie:
– Begründung der Monophylie und Erstellung des Grundmusters der Gesamtgruppe.
– Phylogenetische Beziehungen und rezente Strategien innerhalb der Gruppe.
Evolution:
– Anagenese, Koevolution, Parallelevolution. „Faunenschnitte": Aussterbe-Ereignisse und Neuorganisation: Aufgabe bzw. Erschließung ökologischer Zonen. Evolutive Neuerwerbungen, Radiation.

Historische Entwicklung: das Ergebnis: eine Zusammenfassung der Evolutionsökologie durch die Erdgeschichte.

2. Die frühe Evolution der Hexactinelliden

Die hier vorgestellten paläontologischen Studien fußen auf phylogenetisch-systematischen Studien der Porifera MEHL & REITNER (1991), REITNER (1992) und der Hexactinellida MEHL (1992) sowie auf anderen umfassenden rezentbiologischen Studien der Hexactinellida (MEHL 1992, MEHL & REISWIG, 1991; REISWIG & MEHL, 1991; SALOMON & BARTHEL, 1990; u.a.).

2.1 Jungproterozoikum und frühes Kambrium

Die fossile Überlieferung der Hexatinellida geht auf das Jungproterozoikum zurück. Aus dem Shibatan Member der Dengying Formation im Süden Chinas, stratigraphisch dem Ediacara Member in Australien gleichzusetzen, stammen die frühesten bisher bekannten Poriferenspicula (STEINER et al., 1993). Diese nur im Dünnschliff beobachteten Spicula weisen trotz ihrer starken Umkristallisation deutliche Reste axialer Zentralkanäle auf, deshalb werden sie eindeutig den Porifera zugeordnet. Es handelt sich überwiegend um monaxiale Nadeln, doch finden sich auch einige Stauractine/Hexactine (Paratangentialstrahlen triaxialer Spicula), die eindeutig den Hexactinellida zuzuordnen sind.

Somit sind die Hexactinellida die älteste nachgewiesene, heute noch existente Metazoengruppe auf der taxonomischen Ebene des Subphylums.

Aus der frühkambischen Qiongzhusi-Zone (entspricht dem späten Atdabanium) in Shaanxi, Südwesten Chinas, sind sehr gut erhaltene in-situ-Spiculite mit einer hochdiversen Assoziation isolierter Spicula bekannt (ZHANG & PRATT, 1994): ? Oxyaster und Triaene der Demospongiae, Polyactine der Heteractinida (Calcarea-Stammlinienvertreter) und vor allem viele Nadeltypen der Hexactinellida. Es finden sich sowohl verschiedene Typen regulärer Hexactine, Pinule und vom Pinul abgeleitete Monactine (eine Art Uncinate) als auch Clavule und die stark abgeleiteten Oxystauraster (letztere sind >1 mm große vierstrahlige Oxyhexaster, vgl. MEHL & MOSTLER, in Druck). Wie auch von ZHANG & PRATT (1993) angenommen, handelt es sich bei dieser außergewöhnlich guten kieseligen Erhaltung frühkambrischer Spicula um ein Fossilisationsfenster. Die Poriferen hatten im frühen Kambrium wahrscheinlich eine wesentlich weitere Verbreitung als ihre jetzige,
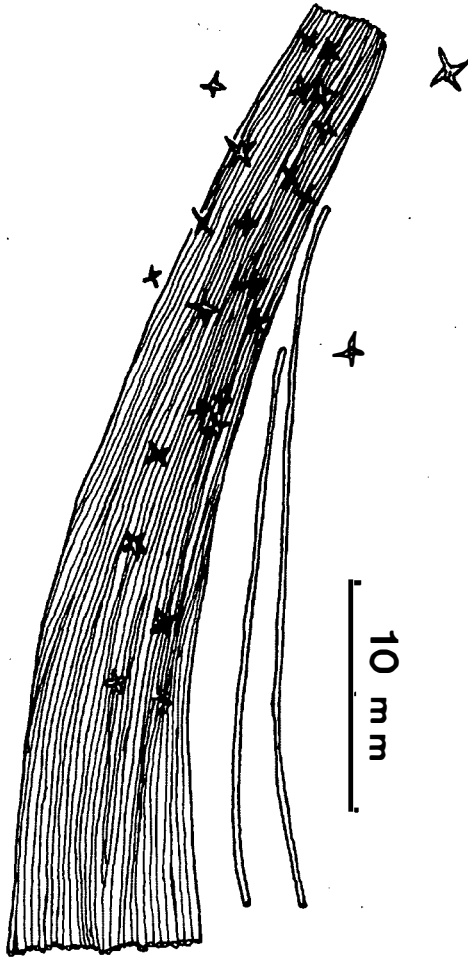
Abb. 1: Hexactinellid aus dem Tommotium von Sansha: *Hyalosinica archaica* MEHL & REITNER, 1993.

lückenhafte Überlieferung vermuten läßt. Auch zeigt die frühkambrische Verbreitung aller drei Poriferen-Großgruppen Hexactinellida, Demospongiae und Calcarea, daß die Porifera eine sehr alte und konservative Gruppe der Metazoa sind.

2.1.1 Die Spongien aus Sansha

Die ältesten bisher bekannten körperlich erhaltenen Poriferen stammen aus dem basalen Kambrium des Profils nahe dem Sansha Traffic Checkpoint (Tommotium der Yangtze-Plattform im N-Hunan). Sie sind von MEHL & REITNER, in STEINER et al. (1993), und von MEHL & ERDTMANN (1994) beschrieben. Die Schwammfossilien sind als braune Krusten, wahrscheinlich Relikte des ehemaligen Weichkörpers, auf den hell angewit-

terten Schichtflächen erkennbar, und sie zeigen verkieselte Spicula und deren Abdrücke. Es handelt sich vorherrschend (vielleicht ausschließlich?) um Hexactinellida in einer erstaunlichen Formenvielfalt, die einige bis heute anhaltende Trends der Hexactinelliden-Evolution bereits erkennen läßt. Die wichtigsten dieser neuen Taxa sollen deshalb an dieser Stelle besprochen werden.

Hyalosinica archaica MEHL & REITNER, 1993
(Abb. 1)

Von dieser Art sind bisher nur Bruchstücke des Stiels bekannt. Es handelt sich um einen Schopf aus langen, im Uhrzeigersinn gewundenen Wurzelspicula (der bisher längste, jedoch unvollständige Schopf des Holotyps ist 5,5 cm lang). Durch dieses Glasfaserprinzip entsteht eine sehr widerstandsfähige und zugleich geschmeidige Struktur. Ein solcher biegsamer Stiel als Anpassung an die Wasserströmung wurde innerhalb der Hexactinellida öfters konvergent entwickelt. Zumindest sind verschiedene, wahrscheinlich nicht näher verwandte Hexactinelliden-Gruppen durch einen solchen Stiel gekennzeichnet: außer *Hyalosinica* beispielsweise auch *Retifungus* (Devon), *Hyalostelia* (Karbon) und *Hyalonema* (Amphidiscophora, Oberkreide–Rezent); (bei *Hyalosinica* sind die langen Nadeln des Stiels im Uhrzeigersinn, bei *Retifungus* und *Hyalonema* dagegen im Gegenuhrzeigersinn gewunden). Der Besitz eines solchen spezialisierten Stiels ist ein abgeleitetes Merkmal, das eine ideale Anpassung an wechselnde Strömungsrichtungen darstellt, damit der Schwamm mit seinem Kanalsystem immer in der Strömung eingeregelt sein kann, wodurch seine filtrierende Ernährung von der Wasserströmung unterstützt wird. Außerdem hält der lange Stiel den Schwammkörper in einer gewissen Höhe über der Sedimentoberfläche, was insbesondere bei feinkörnigem Sedimenteintrag, eventuell innerhalb nepheloider Wasserströmungen sowie bei anoxischen Bodenverhältnissen, wie sie in Chengjiang und Sansha geherrscht haben dürften (ERDTMANN et al., 1994), von Vorteil ist. Durch *Hyalosi-*

nica archaica wissen wir jetzt, daß diese Anpassung bereits im frühen Kambrium entwickelt war.

Sanshadictya microreticulata
MEHL & REITNER, 1993
(Abb. 2)

Diese Art wurde anhand eines einzigen Exemplars beschrieben, das jedoch die entscheidenden dictyospongioiden Merkmale aufweist: eine dünne Wand aus Diactinen und Stauractinen in regelmäßiger zweidimensionaler quadratischer Anordnung. Insgesamt drei Größenordnungen quadratischer Maschen sind vorhanden. Es entspricht der Organisation, die später bei den vor allem aus dem Devon von New York bekannten, retikulaten Dictyospongiidae HALL, 1884, auftritt. Ob es sich hierbei um eine Homologie handelt, ist jedoch unsicher. Die äußerst feine Retikulation in *Sanshadictya* (Maschenweite max. ca. 1 mm) unterscheidet sich von den späteren, viel gröberen Formen, was jedoch für die Systematik wenig signifikant ist. Aus dem Kambrium sind, trotz der relativ vielen mittelkambrischen Funde aus dem Burgess Shale, Wheeler Shale, u.a. bisher keine weiteren Formen von dictyospongioider Retikulation bekannt.

Triticispongia diagonata
MEHL & REITNER, 1993
(Abb. 3)

Dieser Schwamm ist nur 1 cm groß, und seine Spicula messen nur ca. 0,5–1,5 mm. Er besitzt ausschließlich Stauractine in diagonaler Anordnung (vereinzelt mit einem kleinen Loch des „dritten" Axialfilaments im Achsenkreuz, die den triaxialen Ursprung der Stauractine andeuten). Bisher sind nur zwei Exemplare von *Triticispongia* gefunden worden, und wahrscheinlich sind diese Schwämme juvenil. Es handelt sich mutmaßlich um einen Vorläufer der mittelkambrischen *Diagoniella* RAUFF, 1894 (Protospongiidae), der ebenfalls durch Stauractine in diagonaler Anordnung gekennzeichnet ist (Taf. III, Fig. 1). Da alle bisher
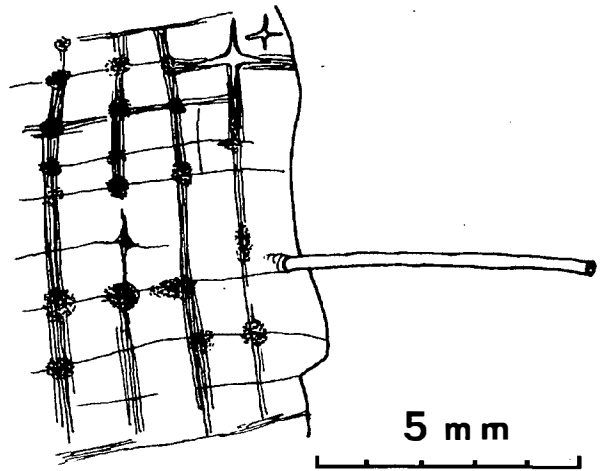

Abb. 2: Hexactinellid aus dem Tommotium von Sansha: *Sanshadictya microreticulata* MEHL & REITNER, 1993.
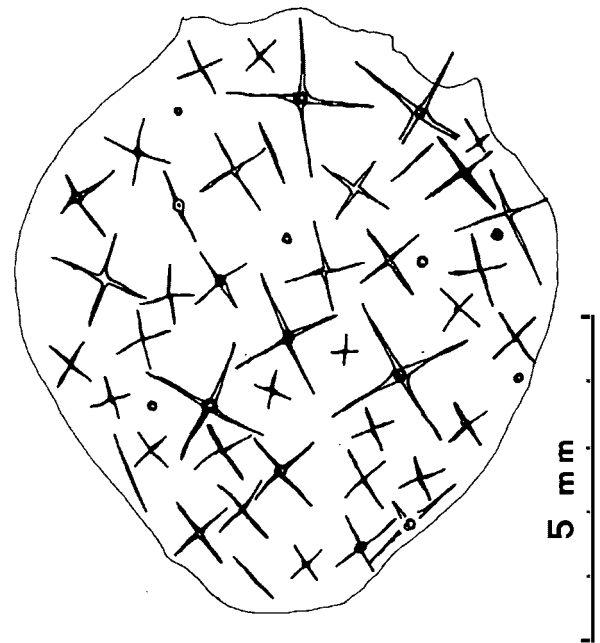

Abb. 3: Hexactinellid aus dem Tommotium von Sansha: *Triticispongia diagonata* MEHL & REITNER, 1993.

beobachteten juvenilen Hexactinelliden mit stauractinen Larvalspicula ausgestattet waren (OKADA, 1928; IJIMA, 1903, 1904) und sich ihre Spikulation im Laufe der Ontogenese stark ändern kann, ist eine sichere systematische Zuordnung der Jungschwämme oft nicht möglich. Da bisher keine größeren eindeutig dieser Art zuordenbaren Exemplare gefunden wurden, weder in Sansha noch in Chengjiang, habe ich diese Formen nicht zu *Diagoniella* gestellt, sondern sie zunächst als eigene Gattung beschrieben.

Sanshapentella dapingi
MEHL & ERDTMANN, 1994
(Taf. VII, Fig. 1)

Von dieser Art liegen bisher drei Exemplare vor. Beim Holotypus handelt es sich anscheinend um ein relativ vollständiges Exemplar, dessen Körperrand großteils erhalten ist. Der Schwamm mißt ca. 25 x 19 mm. Die für diese Art charakteristischen Spicula sind dermale Pentactine mit atrophierten Proximalstrahlen, deren lange Paratangentialstrahlen paarweise angeordnet und alle in dieselbe Richtung „umgebogen" sind. Diese Pentactine sind randlich so orientiert, daß die ca. 3,5 mm langen Paratangentialstrahlen in den Schwammkörper hineinragen, während die kurzen Distalstrahlen anscheinend ursprünglich aus der Dermalmembrane hervortraten. Innerhalb des Schwammkörpers sind Diactine und Stauractine in allen Größen zwischen 0,5 und 7 mm erkennbar (manche Stauractine zeigen im Axialkreuz ein kleines rundes Loch, das einen ursprünglich vorhandenen zentralen Strahl andeutet). Der Paratypus für Sanshapentella dapingi, wurde ursprünglich von MEHL & REITNER (in STEINER et al., 1993) als ?Hunanospongia sp. beschrieben. Nachdem zwei weitere Exemplare, davon ein relativ vollständiges, derselben Art gefunden worden waren, konnte sichergestellt werden, daß es sich hierbei nicht um Hunanospongia handelt, und die Aufstellung einer neuen Gattung Sanshapentella wurde somit erforderlich (MEHL & ERDTMANN, 1994). Die Typusart von Hunanospongia, H. delicata QIAN & DING, 1988, ist nur anhand isolierter Spicula bekannt. Diese sind sehr kleine (0,3–0,5 mm) Hexactine und Pentactine, deren Paratangentialstrahlen alle in eine Richtung gebogen sind, ähnlich wie bei den fast um ein Zehnfaches größeren Dermalspicula von Sanshapentella. Die Typusexemplare Hunanospongia zeigen jedoch alle einen vollständig ausgebildeten Proximalstrahl, der mitten zwischen den Paratangentialstrahlen herausragt. Ein solcher mittiger Strahl fehlt Sanshapentella, deren Paratangentialstrahlen paarig angeordnet und verhältnismäßig sehr viel länger sind. Möglicherweise sind jedoch Sanshapentella und Hunanospongia nahe verwandte Gruppen und bilden ein seit dem Kambrium ausgestorbenes Monophylum. Der spezielle Megasklerentyp mit umgebogenen Paratangentialstrahlen ist in kambrischen Sedimenten (z.B. des Georgina Basins) recht häufig, aber von keinem rezenten Hexatinelliden bekannt. Sehr ähnliche Spicula, nämlich Stauractine mit langen, umgebogenen Paratangentialstrahlen, sind jedoch in einem fragmentarisch erhaltenen kretazischen Schwamm gefunden worden. Es handelt sich um einen neuen lyssakinen Hexactinelliden aus dem Coniac des Arnagerkalks (Bornholm, Dänemark), der bisher in drei Exemplaren vorliegt. Diese Form wurde zunächst mit offener Nomenklatur als Lyssakiner inc. sed. beschrieben (MEHL, 1992: S. 101, Text-Abb. 24). Die umgebogenen Paratangentialstrahlen des Arnager-Hexactinelliden sind jedoch, im Gegensatz zu denen von Sanshapentella, radial angeordnet und ragen aus dem Inneren des Schwammkörpers hervor. Bei der bekannten Konvergenzanfälligkeit dermaler Spicula (MEHL 1991, u.a.) und auch angesichts der großen zeitlichen Lücke (Frühkambrium bis Oberkreide) ist trotz der morphologischen Ähnlichkeit der beiden Nadeltypen eine Homoplasie sehr wahrscheinlich.

Solactiniella plumata MEHL & REITNER, 1993
(Abb. 4)

Diese Art scheint Sansha anscheinend relativ häufig zu sein. Außer dem in STEINER et al. (1993) beschriebenen Holotypus sind in einer späteren Aufsammlung durch ERDTMANN noch weitere Exemplare gefunden worden (MEHL, unveröff. Obs.). Die Spicula sind überwiegend in radialer, an der Peripherie auch plumoser (blumenstraußartiger) Anordnung. Bisher wurden in Solactiniella plumata nur Diactine und vereinzelt fragliche Stauractine beobachtet. Der hexactinellide Status dieser Art ist somit noch nicht absolut gesichert, sie ist jedoch aufgrund der extrem groben Spikulation, die wir nur von den Hexactinellida kennen, sehr wahrscheinlich. Falls sich diese Zuordnung bestätigt, ist Solactiniella der erste Vertreter einer bis heute durchgehenden, paraphyletischen Gruppierung lyssakiner Hexactinelli-
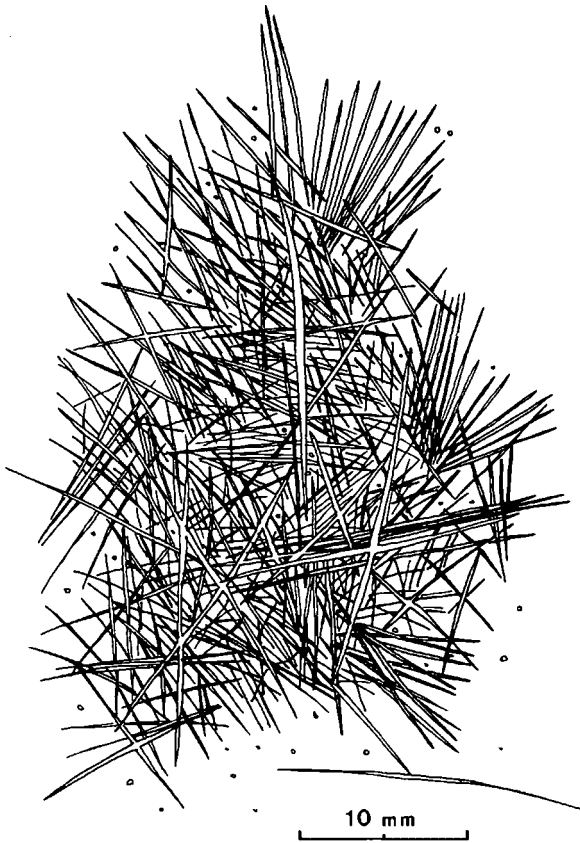
Abb. 4: Hexactinellid aus dem Tommotium von Sansha: *Solactiniella plumata* MEHL & REITNER, 1993.

den. Diese konservativen Formen, die durch dichte Bündel diactiner Spicula in unregelmäßiger Orientierung ausgezeichnet sind, werden hier als „Rossellimorpha" bezeichnet.

2.1.2 Die Gruppierung „Rossellimorpha"

Es ist wichtig festzustellen, daß mit dem Namen „Rossellimorpha" **kein** natürliches monophyletisches Taxon gemeint ist. Bezeichnet wird damit jener große, durch Autapomorphien nicht auflösbare „Pool" an fossilen und rezenten Hexactinelliden, die nur durch plesiomorphe Merkmale charakterisiert sind, also bestenfalls eine paraphyletische Gruppierung bilden. Von ähnlicher Organisation sind nach eigener Beobachtung die meisten, wenn nicht sämtliche, der aus Chengjiang (Yunnan, China) stammenden Spongien (Atdabatium-Alters, also nur wenig jünger als die Fauna von Sansha). Einige dieser Spongien

wurden von CHEN et al. (1990) als Demospongiae einer neuen Gattung *Quadrolaminiella* beschrieben. Nach der Größe und Anordnung der Spicula zu urteilen, dürfte es sich hierbei jedoch um Hexactinellida handeln. Außerdem sind in einem Exemplar auch Stauractine festgestellt werden (MEHL, unveröff. Obs.). Die rossellimorphe Organisation ist somit ein sehr alter hexactinellider Bauplan. Es handelt sich um relativ dickwandige lyssakine Formen, häufig mit Wandlücken versehen, deren Spicula überwiegend zu Diactinen reduziert und in unregelmäßiger Orientierung, häufig tangential zu den Außenporen, sind. Aus diesem uralten Grundplan sind im Laufe der Erdgeschichte immer wieder ähnliche Formen hervorgegangen, beispielsweise die Rufospongidae n. fam. (=*Rufospongia/Taleolaspongia/Bulbospongia*-Gruppe) aus dem Mitteldevon; (RIGBY & MEHL, in Druck, Text-Abb. 9). Heute noch ist diese Skelettarchitektur innerhalb der lyssakinen Hexactinellida weit verbreitet, wie bei den meisten Amphidiscophora SCHULZE, 1887, und bei den Rosselliidae SCHULZE, 1887. Eine solche Formengruppe (hier: die „Rossellimorpha"), deren Position innerhalb eines bestimmten Monophylums (hier: die Hexactinellida) aufgrund ihrer Armut an abgeleiteten Merkmalen unsicher ist, wird adokimische Gruppe (gr. *adokimos* = unecht) genannt (BÖGER, 1989). Die „Rossellimorpha" stellen den ultrakonservativen Grundstock dar, aus dem sich im Laufe der Erdgeschichte abgeleitete Merkmale immer wieder entwickelten. Wahrscheinlich konnte der „rossellimorphe" Grundplan derart konservativ bleiben, weil sich die Umweltbedingungen der Habitate dieser Schwämme wenig veränderten. An geringere Tiefen und bewegtes Wasser angepaßte Hexactinelliden, die sich im Laufe der Erdgeschichte immer wieder entwickelt haben, waren vergleichsweise kurzlebige, durch abgeleitete Merkmale gekennzeichnete Gruppen.

2.2 Die Taphonomie mittelkambrischer Fossilisationsfenster

Das mittlere Kambrium ist eine Zeit starker Radiation der Hexactinellida. Wahrscheinlich wur-
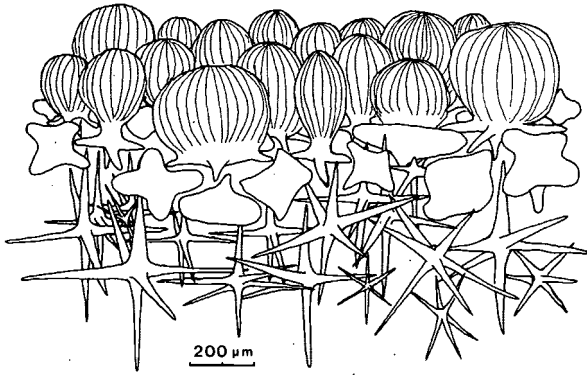
Abb. 5: Hypothetische Rekonstruktion des Sklerenskeletts von *Thoracospongia follispiculata* n. g., n. sp. (anhand isolierter Spicula aus dem mittelkambrischen Georgina Basin, Australien); Beschreibung siehe Anhang.

den durch diese Schwämme neue ökologische Zonen erfolgreich geschaffen, wobei verschiedene Strategien „ausprobiert" wurden. Wir haben aus dieser Zeit einige Fossilisationsfenster, z.B. den Burgess Shale, (Kanada) und den Wheeler Shale (Utah, USA), wo die Schwämme in ausgezeichneter körperlicher Erhaltung vorliegen. Diese Erhaltung ist das Ergebnis schneller Einbettung durch die feinste Tontrübe von Schüttungsereignissen. Die Spongien der Burgess-Shale-Platten zeigen häufig sowohl arten- als auch größenmäßig eine diskrete Verteilung: Auf einer nur ca. 5 x 7 cm großen Platte befinden sich beispielsweise über 30 Exemplare von *Choia ridley* WALCOTT (Demospongiae), alle in der Größenordnung von maximal 1 cm (Taf. VI, Fig. 3). Zur Erklärung dieses Sortierungseffekts wird ein schonender Transport mit dem sehr feinkörnigen distalen Abschnitt eines Trübstroms, der durch einen Sturm oder Sedimentrutschung ausgelöst wurde. Ähnliche Sedimentationsmechanismen sind auch für die ausgezeichneten frühkambrischen Fossil-Lagerstätten von China, z.B. in Chengjiang, verantwortlich , wo die plötzliche Einbettung wahrscheinlich durch Tempestite verursacht wurde (ERDTMANN et al., 1994; HOU et al., 1991). Möglich wäre jedoch auch eine sehr schnelle Einbettung im Zusammenhang mit trübstofffreien Nepheloidlagen, wie sie rezent vorwiegend in der Tiefsee beobachtet werden (BISCAYE & EITTREIM, 1977; EITTREIM et al., 1976), jedoch auch aus Wassertie-

fen von 15–70 m beschrieben sind (ZOUTENDYK & DUVENAGE, 1989).

Die Spongien des Burgess Pass (Kanada) wurden erstmalig von WALCOTT (1920) beschrieben und später von RIGBY (1986) neu bearbeitet. Aus dieser Lokalität kennen wir einige vorzüglich erhaltene Hexactinelliden. Die Protospongiidae sind hier mit den Arten *Protospongia hicksi* WALCOTT und *Diagoniella hindei* WALCOTT vertreten. Es finden sich aus dem Burgess bzw. Wheeler Shale auch die ersten typischen „Rossellimorphen", wie *Stephenospongia magnipora* RIGBY, 1986, und *Ratcliffespongia wheeleri* RIGBY & CHURCH, 1990, mit feinen, großteils diactinen Nadeln, die tangential um ovale Wandlücken herum angeordnet sind.

2.3 Spicula aus dem Georgina Basin
(Taf. I; Taf. II, Fig. 1–7; Taf. III, Fig. 4–5; Taf. IV, Fig. 2; Taf. VII, Fig. 4; Abb. 5)

Aus dem Mittelkambrium des Georgina Basins (Südaustralien) stammt eine gut erhaltene Fauna, die unter anderem isolierte Sklerite von Chancellorien und Poriferenspicula enthält, welche derzeit noch durch die Autorin in Arbeit sind. An Poriferen finden sich außer octactinen und hexiradiaten ?*Eiffelia*-Nadeln der Heteractinida diverse Spicula der Demospongiae. Diese sind z.B. dendroclone Desmen (wahrscheinlich von *Rankenella mors* GATEHOUSE, 1968, der früheste als Körperfossil dokumentierte „Lithistide", ebenfalls aus dem Georgina Basin; KRUSE, 1983). An Mikroskleren sind Sigmen und (wahrscheinliche) Oxyaster vorhanden. Außerdem gibt es eine reiche Assoziation hexactinellider Spicula. Unter anderem sind viele, teilweise mehrere Millimeter große Clavule vertreten, davon **eine** mit terminal abgestumpftem Distalende (Taf. I, Fig. 1). Es handelt sich hierbei um den bisher frühesten Vertreter dieses Spiculatyps, der ansonsten nur aus dem späten Kambrium von Iran bekannt ist und zur Aufstellung der Art *Nabaviella elegans* MOSTLER & MOSLEH-YAZDI, 1976, führte. Außerdem findet sich ein eigenartiger Nadeltyp, der hier als **Kometiaster** bezeichnet werden soll. Es sind Triaxone, bei denen ein bis

drei Hauptstrahlen in eine große Zahl bedornter, S-förmig geschwungener Sekundärstrahlen aufgespalten sind (Taf. III, Fig. 4–5). Sicher stehen diese Hexaster-ähnlichen Spicula mit der aus dem Ordovizium ebenfalls nur als isolierte Nadeln bekannten Art *Kometia cruciforme* in einer phyletischen Linie. Ein neuer, sehr massiger Typ (wahrscheinlich) dermaler Pinule wird hier zu einer neuen Art Art *Thoracospongia follispiculata* (siehe Anhang; Taf. II, Fig. 1–7; Abb. 5) gestellt. Zur äußeren Cortex dieser Schwämme gehörten möglicherweise außerdem die in denselben Proben häufigen, extrem geschwollenen Triaxone: Hexactine, Pentactine und vor allem Stauractine sowie Diactine (Taf. IV, Fig. 2; Taf. I, Fig. 2–8; Taf. VII, Fig. 4). Warum die Schwämme im Kambrium derart massige, panzerähnliche Dermalspicula entwickelten, ist unbekannt. Da sie aller Wahrscheinlichkeit nach nur unter Ruhigwasserbedingungen lebten, scheint eine Stabilisierung des Schwammskeletts einer äußeren Turbulenz gegenüber kaum entscheidend gewesen zu sein. Möglicherweise dienten solche massiven Dermallagen dem Schutz gegen irgendwelche Räuber (z.B. schwammfressende Fische oder weidende Mollusken).

3. Die Hexactinelliden-Evolution im Altpaläozoikum

3.1 Spätkambrium

Aus dem späten Kambrium sind die Hexactinellida fast ausschließlich aufgrund isolierter Spicula bekannt, und die Funde erscheinen im Verhältnis zu den mittelkambrischen Vorkommen vergleichsweise arm. Recht diverse Spicula-Vergesellschaftungen sind aus dem Spät-Kambrium von Iran (MOSTLER & MOSLEH-YAZDI, 1976) und aus Queensland (BENGTSON, 1986) bekannt. Manche Spiculatypen, z.B. die als *Nabaviella elegans* MOSTLER & MOSLEH-YAZDI publizierten „Hemidisken" mit einer distalen, klumpenartigen Verdickung, sind jetzt jedoch auch aus dem mittelkambrischen Georgina Basin (s. u.) nachgewie-

sen. Die bekannten Assoziationen spätkambrischer und ordovizischer Hexactinelliden-Spicula sind sehr ähnlich. Aus dem Kambrium von Queensland stammen Propeller-ähnliche Pinule (Dermalspicula), *Konyrium mariae* BENGTSON und eigenartige Häkchen-Skleren (*Silicunculus australiensis* BENGTSON), die möglicherweise frühe Wurzelspicula sind. Dem *Silicunculus australiensis* sehr ähnliche Formen sind z.B. auch aus dem Ordovizium bekannt (WEBBY & TROTTER, 1993). Aus dem Spätkambrium hat BENGTSON (1986) bemerkenswerte, nur ca. 250 μm große, anscheinend aus einem rigiden Gerüst von triaxialen Spicula bestehende „Kugeln" mit einem großen zentralen Hohlraum unter dem Namen *Echidnina runnegari* beschrieben. Diese werden vom Autor als spiculäre Hüllen von Larven oder Gemmulae hexactinellider Schwämme interpretiert. Sowohl Larven mit rigiden Skeletten, als auch irgendwelche Gemmulae sind jedoch ansonsten von den Hexactinellida unbekannt. Am ehesten erinnern die Kugeln an rigide Knospen, allerdings ohne ersichtliche Spuren einer ehemaligen Anheftung, die bei Knospen vorhanden sein müßten. Rigide Knospen von ca. 500 μm Durchmesser sind von den rezenten, im Adultzustand nicht-rigiden Rosselliidae bekannt (z.B. *Staurocalyptus glaber* IJIMA, 1897; vgl. MEHL, 1992).

Falls es sich bei *Echidnina runnegari* wirklich um Schwämme handelt, und nicht etwa um Radiolarien (was nicht auszuschließen ist) sind sie vielleicht als planktonische Rhagons (Jungschwämme) zu deuten. Dies jedoch wäre eine bisher unbekannte, eigenständige Verbreitungsstrategie innerhalb der Porifera (vgl. REITNER, 1992).

3.2 Ordovizium

Die Vorkommen ordovizischer Hexactinelliden, wie bereits die des Spätkambriums, erscheinen im Vergleich zur mittelkambrischen Formenfülle relativ verarmt. Dieser Eindruck liegt vor allem daran, daß aus dem Ordovizium nur relativ wenige körperlich erhaltene Hexactinelliden beschrieben sind. Im Ordovizium war jedoch die gesamte Bandbreite paläozoischer Hexactinelliden

in großer Vielfalt entwickelt. Viele körperlich erhaltene Vertreter der Protospongiidae aus dem Ordovizium von Little Métis (Kanada) finden sich unter den von DAWSON, 1888 und 1889 (in DAWSON & HINDE, 1888 und 1889; vgl. „nomenclatural note" von CLARK, 1982), beschriebenen Arten. Das Studium des Typusmaterials dieser Taxa ist jedoch erschwert, da DAWSON (zu Dokumentationszwecken) die Fossilien mit weißer Farbe bemalt hat. Die weißen Linien und Kreuze sind in der Regel neben, teilweise aber auch über den pyritisierten, ohnehin schwer erkennbaren Spicula aufgebracht. Die von DAWSON (1889) wiedergegebenen bemalten Typen sind darüber hinaus z.T. erheblich ergänzt worden. So wurden viele „Spicula" einfach dazugemalt (vgl. Taf. III, Fig. 2). Die im Redpath Museum, Montreal, befindliche DAWSON-Sammlung enthält vorwiegend Vertreter der Protospongiidae *sensu stricto*, darunter auch Exemplare, an deren stauractinen Spicula (trotz der Bemalung) die triaxiale Natur erkennbar ist (vgl. Absatz über die Protospongiidae). Ein weiteres, vergleichbares Beispiel aus dem Ordovizium ist die protospongiidae Art *Asthenospongia acantha*, RIGBY et al. (1981), die überwiegend Stauractine, jedoch auch einige Hexactine besitzt.

Als früheste eindeutig dictyospongioide Form (von dem kleinen Fragment, *Sanshadictya microreticulata*, aus dem Tommotian abgesehen) ist *Tiddalickia* RIGBY & WEBBY, 1988, aus dem späten Ordovizium anzuführen, die gleich von zwei Lokalitäten bekannt ist: *T. quadrata* RIGBY & WEBBY, 1988, aus Australien und *T. manitobensis* RIGBY & LEITH, 1989, aus Manitoba, Kanada. Aus dem Ordovizium kennen wir ferner einige morphologische Übergangsformen zwischen dem protospongioiden und dem dictyospongioiden Bauplan. Ein Beispiel dafür ist *Cyatophycus* WALCOTT, 1879, der innerhalb eines dictyospongioiden, retikulären Skeletts aus Diactinen noch viele Stauractine aufweist. Es gibt aus dieser Zeit jedoch noch weitere Formen, die sich schwer einem der Hexactinelliden-Großtaxa zuordnen lassen. *Wareembaia concentrica* RIGBY & WEBBY, 1988, besitzt eine diktyonale Dermallage von zwei bis drei Schichten aus verlöteten Triaxonen. Darunter liegen die Hexactine in irregulärer, nicht-rigider

Anordnung. Die äußerste dermale Hexactinenschicht ist durch kugelig geschwollene Distalstrahlen, regelmäßig wie Perlen auf einer Schnur aufgereiht, gekennzeichnet. Bei genauer Betrachtung der Nahaufnahme dieser Dermalseite (RIGBY & WEBBY, 1988: Pl. 43, Fig. 2) scheint das Skelett jedoch nicht der kubischen Verschmelzung von Hexactinen eines echten Diktyonalgerüstes zu entsprechen. Eher erinnert es an eine Verlötung durch Synapticula, analog manchen lyssakinen Hexasterophorida (z.B. *Euryplegma auriculare* SCHULZE, 1887). Die Autorin möchte deshalb *Wareembaia* derzeit nicht zu den Hexactinosa *s. str.* rechnen (vgl. hierzu auch MEHL & MOSTLER, 1993). Erneute Untersuchungen des in Sydney befindlichen Typusmaterials zu RIGBY & WEBBY (1988) sollen diese Frage endgültig klären.

Die Gattung *Brachiospongia* MARSH, 1867, namengebend für die Brachiospongiidae BEECHER, 1889, ist ab dem späten Ordovizium nachgewiesen. Außer der Typusart *Brachiospongia digitata* (OWEN, 1858) (Taf. VI, Fig. 1) wurden aus dem Ordovizium von Kentucky noch viele Arten dieser Gattung beschrieben, die sich von der Typusart nur in makroskopischen Merkmalen, wie Körpergröße oder Zahl der Arm-ähnlichen Fortsätze, unterscheiden. Wahrscheinlich gehören diese „Arten" zum Teil in die Variationsbreite von *B. digitata*; dies könnte z.B. für *B. minimus* JILLSON, 1953, der Fall sein.

Die hexactinellide Großgruppe Hexasterophora ist seit dem basalen Ordovizium nachgewiesen: Die ältesten bisher bekannten Oxyhexaster stammen aus dem tiefen Ordovizium Schwedens (MOSTLER, 1986). Geschiebeblöcke von Braderup, Sylt (tiefes Mittelordovizium), enthalten nach eigenen Beobachtungen in der Sammlung VON HACHT bereits verschiedene Oxyhexastertypen.

3.3 Palökologie der Poriferen im Ordovizium und das Problem der selektiven Überlieferung

Die Dokumentation der Hexactinellida des Ordoviziums ist überwiegend auf isolierte Spicula

aus Lösungsrückständen beschränkt. Wie im folgenden verdeutlicht werden soll, dürfte das weitgehende Fehlen vollständiger Schwämme, seit dem späten Kambrium bemerkbar, vor allem auf mangelhafte Überlieferung zurückzuführen sein. Zwei Beispiele spongienführender Schichten des tieferen Ordoviziums wurden daraufhin untersucht: 1) Geschiebe aus dem *Obulus*-Sandstein des tiefen Mittelordoviziums von Braderup, Sylt (im Zusammenarbeit mit VON HACHT, Hamburg); 2) das frühe Ordovizium der San-Juan-Formation in der Präkordillere, Argentinien, die bisher reichste Spongienlokalität des Ordoviziums von Südamerika (in Zusammenarbeit mit LEHNERT, Arbeitsgruppe BUGGISCH, Univ. Erlangen).

ad 1) Im Geschiebe, besonders aus dem Glimmersand von Sylt, sind vollkörperlich erhaltene Spongien sehr häufig (z.B. VON HACHT, 1987, und 1987a). Nach eigenen Beobachtungen in der spongienreichen Grube 3 in Braderup auf Sylt sowie in den Privatsammlungen LANGE und VON HACHT findet sich dort eine sehr reiche Vergesellschaftung Desmen-tragender Demospongiae („Lithistida"), vereinzelt auch isolierte hexactinellide Wurzelschöpfe, aber kein einziger vollständiger hexactinellider Schwamm. Studien herausgelöster Spicula aus dem Kaolinsandstein ergeben jedoch einen anderen Befund: Geschiebeblöcke des basalen Mittelordoviziums enthalten fast ausschließlich Hexactinelliden-Spicula. Diese Faunen sind recht divers und enthalten außer Hexastern unter anderem auch Stauractine, Oxyhexaster, Uncinate und diverse Ankerspicula. Ab dem Mittelordovizium treten erstmals monocrepide Desmen von den Anthaspidellidae („Lithistida") und anderen Demospongiae-Nadeln in großer Formenfülle auf, gleichzeitig sind die Hexactinelliden fast völlig verschwunden. Diese Verteilung weist auf eine Verflachung im Mittelordovizium hin und läßt sich mit der allgemeinen Regression auf der Scano-baltischen Plattform ab dem mittleren Caradoc (OPALINSKI & HARLAND, 1981; OWEN et al., 1990) gut korrelieren.

ad 2) Aus dem Mittelordovizium der San-Juan-Formation ist eine reiche „Lithistiden"-Fauna bekannt; die Hexactinellida waren bisher nur von Wurzelschöpfen und isolierten Hexactinen, die

Heteractinida nur von einem einzigen isolierten Octactin bekannt (BERESI & RIGBY, 1993). Aus den zahlreichen Proben aus verschiedenen ökologischen Bereichen, die durch LEHNERT mit Hilfe von Conodonten datiert wurden, waren nur wenige spiculaführend. Die nur sporadische (fensterartige) Erhaltung der Skleren wird dadurch deutlich, daß z. B. Schlämmproben aus Schichten des höchsten Arenigs – basalen Llanvirns, die sehr reich an körperlich erhaltenen Schwämmen sind, überhaupt keine isolierten Nadeln geliefert haben. Die Analyse der wenigen spiculaführenden Lösungsrückstände läßt jedoch interessante Rückschlüsse über die Ökologie der Spongien zu. Die höchstdiverse Spicula-Zusammensetzung weist eine Probe aus Schwamm-, Algen-, Stromatoporoiden-Plattformriffen des Spät-Arenigs auf. Sie enthält viele Oxen und diverse Typen der Triaene, zusammen mit zahlreichen verschiedenen Typen der Octactine. Es sind also die Demospongiae und die Heteractinida in großer Formenfülle vertreten. In den gleichaltrigen hochenergetischen Bereichen der Plattform, in denen nur Stromatoporoidenriffe auftreten, finden sich ausschließlich Heteractiniden. Die Interplattform-„Becken" (Llanvirn, Llandeilo) zeigen eine relativ wenig diverse Assoziation, die nur aus Hexactinelliden besteht. Aus dieser Verteilung ergibt sich für das frühe und mittlere Ordovizium dieser Region eine sehr scharfe Ökozonierung durch die Poriferen: Die Heteractinida finden sich in den Bewegtwasserzonen, in den etwas ruhigeren Interriff- und Patch-Reef-Bereichen treten diese zusammen mit einer reichen Demospongiaefauna, unter anderem Desmen-tragenden Formen, auf. Die Ruhigwasser-, Slope- bis Interplattform-Bereiche enthalten ausschließlich hexactinellide Schwämme. Diese „Becken" waren wahrscheinlich relativ flach, jedenfalls nicht mit der heutigen abyssalen Zone vergleichbar. Aufgrund der im Ordovizium wahrscheinlich noch relativ flachen Oxykline der Ozeane dürfte in der anoxischen Tiefsee noch kein benthisches Leben möglich gewesen sein.

Bei der Ökozonierung mit Hilfe von Schwammnadeln ist große Vorsicht geboten. Rezent-Beobachtungen aus der Arktis und dem Mittelmeer haben ergeben, daß die Spicula-Verteilungen in

keinem Fall die ursprüngliche Poriferenfauna genau widerspiegelten, sondern immer durch selektive Lösungsvorgänge und Transport stark verfälscht waren (REITNER & MÜLLER-WILLE, 1993; LINDENBERGER, 1993). Die Verteilung isolierter Spicula kann bestenfalls für qualitative, nicht aber quantitative Aussagen über die ursprüngliche Biocoenose herangezogen werden. Unter Berücksichtigung der Sedimentologie und der übrigen Fauna, vor allem auch der körperlich erhaltenen Schwämme, geben die isolierten Spicula manchmal doch nützliche Hinweise sowohl auf Taphonomie als auch Palökologie eines Ablagerungsraumes.

Innerhalb der San- Juan-Formation ist die Spicula-Verteilung so eindeutig, daß unter Berücksichtigung der Körperfossilien eine Spongienzonierung gerechtfertigt ist. Die Befunde aus den Proben des mittelordovizischen Kaolinsandsteins von Braderup, wo sich Demospongiae und Hexactinellida gegenseitig weitgehend ausschließen, scheinen diese Ökozonierung zu bestätigen. Sekundäre Lösungsprozesse, die innerhalb verschiedener Environments selektiv zwischen Kieselnadeln der Demospongiae und der Hexactinellida diskriminieren könnten, wären als Ursache des gegenseitigen Ausschließens beider Gruppen jedoch denkbar. Eine Biozonierung, welche die Hexactinellida weitgehend auf tiefere Slope- und Beckenbereiche beschränkt, könnte für das geringe Überlieferungspotiential körperlich erhaltener Hexactinelliden aus dem Spätkambrium und dem Ordovizium verantwortlich sein. Eine hochdiverse Kieselschwamm-Assoziation der spätordovizischen Malongulli-Formation (New South Wales, Australien) wurde von RIGBY & WEBBY (1988) bearbeitet. Die dort gefundenen körperlich erhaltenen Schwämme stammen aus allochthonen Blöcken von feinkörnigen, Spicula-, Radiolarien-, Graptoliten- und Trilobiten-reichen Sedimenten eines hemipelagischen Environments, das sich im Hangenden einer ertrunkenen Karbonatplattform entwickelte. Die Spongien-Assoziation setzt sich überwiegend aus Desmen-tragenden Demospongiae sowie Hexactinelliden zusammen, nur vereinzelt treten sog. „Sphinctozoen" auf. Es ist bezeichnend, daß die Kieselschwämme, vor allem

die Hexactinellida, immer aus Ablagerungen der Beckenfazies stammen, während die „Sphinctozoen" in Sedimenten eines deutlich höherenergetischen Environments gefunden wurden. RIGBY & WEBBY (1988) führen diese Verteilung darauf zurück, daß die Hexactinelliden und Demospongiae im Interplattformbecken-/Slope-Environment lebten, während die „Sphinctozoen" in flachem Wasser lebten. Die von WEBBY & TROTTER (1993) von derselben Lokalität veröffentlichte Spicula-Assoziation scheint diese Annahme zu bestätigen: Sie stammt aus Blöcken einer Graptolithen-Spicula-führenden Wechsellagerung von pelagischen, siltigen Mergeln und enthält fast ausschließlich hexactinellide Spicula.

3.4 Silur

Aus dem Spätsilur von Skandinavien sind die bisher ältesten zweifelsfreien Amphidisken dokumentiert (MOSTLER, 1986). Somit ist das Taxon Amphidiscophora spätestens ab dem Silur eindeutig nachgewiesen.

3.4.1 Brachiospongiidae und „Rossellimorpha"

Die Brachiospongioidea waren während des Silurs weit verbreitet. Z.B. sind die Pelicaspongiidae RIGBY, 1970, mit *Vaurealispongia* und *Twenhofella* RIGBY, 1974, die bereits im späten Ordovizium einsetzten, auch aus dem Mittelsilur bekannt (RIGBY et al., 1979). Viele Hexactinellida des Silurs stammen aus der kanadischen Arktis, wo die reichsten Lagerstätten silurischer Kieselschwämme vorkommen. Es sind vor allem lithistide Demospongiae, die jedoch manchmal auch mit Hexactinelliden vergesellschaftet sind (DE FREITAS, 1991; u.a.). Beschrieben sind auch einige silurische Arten der durch einen *Hyalonema*-ähnlichen Wurzelschopf gekennzeichneten Gattung *Hyalostelia*, z.B. *H. anticostiana* aus Kanada (TWENHOFEL, 1928). Viele der silurischen Hexactinelliden sind jedoch solche Lyssakine *incertae sedis*, die in dieser Arbeit als „Rossellimorpha" bezeichnet werden. Ein charakteristischer Verteter ist

Malumispongium RIGBY (1967): dickwandig mit großen Wandlöchern, um welche die Triaxone in unregelmäßiger Anordnung gruppiert sind. Weitere Beispiele sind *Lumectospongia* und *Corticulospongia* RIGBY et al., 1989, die überwiegend diactine Megaskleren (bei *Lumectospongia* sind diese Uncinate) aufweisen. Aus dem Holotypus zu *Corticulospongia* haben RIGBY et al. (1989) außerdem Oxyhexaster gefunden, wodurch diese Gattung eindeutig dem Taxon Hexasterophora zugeordnet werden kann.

3.4.2 Reticulosa

Vertreter der retikulaten Hexactinelliden zeigen bereits im späten Silur auffallende Ähnlichkeit mit den Dictyospongiidae *sensu stricto* des Devons von New York. *Dictyospongia apache* RIGBY, 1989, ebenfalls aus dem Mittelsilur der kanadischen Arktis, besitzt ein retikulates Skelett aus Hexactin-abgeleiteten Spicula mit quadratischen Maschen in mindestens vier Größenordnungen. *Protospongia conica* RIGBY & HARRIS, 1979, von derselben Lokalität besitzt eine typisch protospongioide Retikulation; allerdings zeigen einige ihrer „Stauractine" deutliche Knöpfe atrophierter Distalstrahlen (pers. Obs. am Holotypus). Eine andere als *Diagoniella tubulare* RIGBY & HARRIS, 1979, beschriebene Art (aus Silur/Devon-Grenzschichten von Nevada) bedarf der weiteren Erläuterung und Revision. Sie und die Art „*D.*" *nevadensis* RIGBY & STUART, 1988 (ebenfalls Silur/Devon, Nevada), werden hier zu der Gattung *Hexatractiella* n. gen. gestellt (siehe Anhang). Nach eigenen Beobachtungen des Typusmaterials unterscheiden sich die beiden Arten lediglich in der Körperform und in den Dimensionen ihrer Skelettmaschen, ihre Spicula und Skelettarchitektur sind jedoch identisch. Aus denselben Schichten von Nevada wurde vor kurzem eine neue Hexactinelliden-Faunula bearbeitet (MEHL et al., 1993). Dabei stellte sich heraus, daß die bei „*Diagoniella*" *nevadensis* zunächst als Stauractine und Diactine interpretierten Spicula (RIGBY & STUART, 1988) größtenteils, wenn nicht ausschließlich, abgewandelte Hexactine sind. Es wurde ge-

zeigt, daß die prominenten Längszüge vermeintlicher Diactine in Wirklichkeit aus stark abgewandelten Triaxonen mit einem oder zwei extrem verlängerten Paratangentialstrahlen aufgebaut sind (Abb. 6–7; Taf. IV, Fig. 4). Diese Spikulation stellt eine Übergangsform zum dictyospongioiden Typ Skelett dar und ist ein Beispiel dafür, wie aus Hexactinen-tragenden, retikulaten Hexactinelliden die dictyospongiide Organisation entwickelt wurde. Es handelt sich bei den diactinen Nadelzügen der Dictyospongiidae um eine aus Hexactinen entwickelte Spikulation, die mit jener der ausschließlich Stauractinen-tragenden Gattung *Diagoniella* (z.B. *Diagoniella robisoni*; Taf. III, Fig. 1) sicher nicht homolog ist.

Aus den Silur/Devon-Grenzschichten von Nevada stammen einige Arten der Gattung *Gabelia* RIGBY & MURPHY, 1983 (RIGBY et al., 1991). *Gabelia* mit ihrer regulären, protospongioiden Spikulation ist ein weiteres Beispiel aus dieser Zeit für die Entstehung einer retikulären Anordnung von Triaxonen mit der Tendenz zur Bildung longitudinaler Nadelzüge.

3.5 Spongien-Lagerstätten des Devons und die Frasné/Famenne-Grenze

Die Hexactinellida des frühen Devons sind kaum bekannt. Eine Blüte der Hexactinelliden fing erst mit dem Beginn des Frasné an und setzte sich anscheinend über die Frasné/Famenne-Grenze bis in das Mississippian hinein fort. Diese Expansion hängt wahrscheinlich damit zusammen, daß spezialisierte Gruppen der Hexactinellida im späten Devon und Mississippian auch höherenergetische Flachwassergebiete (vgl. z.B. RIGBY & KEYES, 1990) besiedeln konnten. Eine sehr ergiebige Spongien-Fundstelle aus dem Silur/Devon- Grenzbereich ist die oben erwähnte Roberts-Mountains-Formation (Starvation Canyon, Nevada), die außer vereinzelten Demospongien ausschließlich Hexactinelliden der Gruppe Reticulosa geliefert hat. Die Fauna aus dem Starvation Canyon liefert neben wichtigen Daten über protospongiide-dictyospongiide „Übergangsformen" auch interessante Hinweise auf Palökologie und
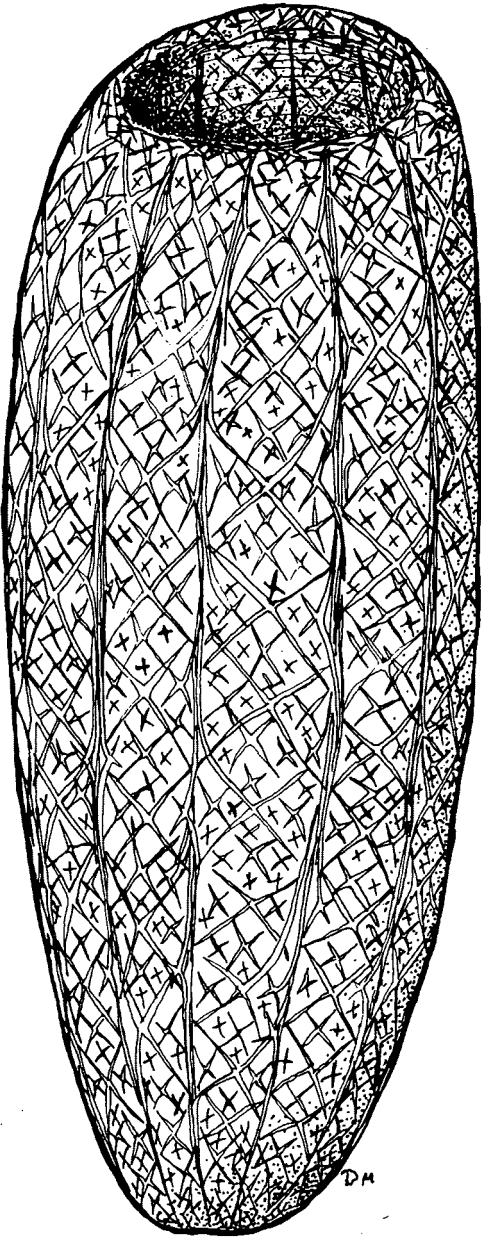
Abb. 6: *Hexatractiella nevadensis* aus Silur/Devon-Grenz-schichten im Starvation Canyon, Nevada, USA. Die Längszüge von Spicula sind aus abgewandelten Hexactinen zusammengesetzt; Beschreibung siehe Anhang.
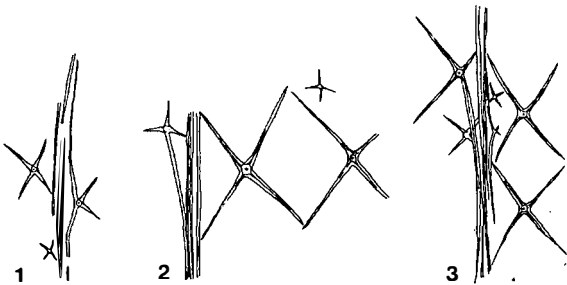

Abb. 7: Detailansicht der longitudinalen Spiculazüge in *Hexatractiella nevadensis*.

Taphonomie dieser Schwämme (MEHL et al., 1993). So läßt sich beispielsweise aus der Verteilung der Schwammfossilien auf den Schichtflächen (Taf. VI, Fig. 2) erkennen, daß die Spongien wahrscheinlich in diskreten, monospezifischen Biocoenosen lebten. Sie sind innerhalb tonreicher Sedimentwolken (vielleicht nur über kurze Abstände) transportiert worden, bevor sie von derselben Tontrübe eine schnelle Einbettung erfuhren (Abb. 12). Eine ähnliche Taphonomie läßt sich für die Lagerstätte im Burgess Shale ableiten (vgl. Taf. VI, Fig. 3)

Aus dem Mitteldevon sind einige Spongien-Lagerstätten bekannt, beispielsweise der Bundenbacher Schiefer (siehe unten) und die sehr reiche Hexactinelliden-Lokalität der Simpson Park Range, Nevada (RIGBY & MEHL, in Druck). Letztere hat Reticulosa geliefert und „Rossellimorpha": z.B. den bisher jüngsten Vertreter der Gattung *Teganiella*, sowie die Rufospongidae n. fam. (= *Rufuspongia-Taleolaspongia-Bulbospongia*-Gruppe) mit großer Affinität zu den rezenten Rosselliiden. Die Taphonomie dieser Schwammfossilien bestätigt die obenstehenden Vorstellungen über die Biocoenosen der Hexactinelliden in diskreten, monospezifischen Clusters (RIGBY & MEHL, in Druck). Aus Mittel/Oberdevon-Grenzschichten von Madfeld (Hessen, BRD) stammt ein Exemplar der Art *Gabelia fascicula* RIGBY et al., 1991 (s. Anhang). Es handelt sich hierbei um den bisher einzigen Fund eines Hexactinelliden der nordamerikanischen Faunenprovinz in Europa. Der Fund zeigt jedoch zugleich, daß die scheinbare Isolation der europäischen von den amerikanischen Faunen vor allem ein Problem fehlender Lagerstätten, aber auch mangelnder Dokumentation der europäischen Hexactinellida sein dürfte. Diese Hypothese wird durch die Revision der hexactinelliden Art *Cyatophycus rhenana* (SCHLÜTER, 1892) aus dem Bundenbacher Schiefer bestätigt (s. u.).

Aus dem Frasné sind sehr viele Hexactinelliden fast aller paläozoischer Gruppen überliefert, nur die Protospongiidae scheinen im Devon endgültig erloschen zu sein. Die Hexactinosa treten erstmalig im Frasné auf, an mehreren verschiedenen Lokalitäten der Welt zugleich (siehe unten). Eben-

falls Frasné-Alters ist *Mattaspongia* Rigby, 1970, aus der Mount Hawk Formation von Alberta. Die Spikulation dieser Form ist für die phylogenetische Ableitung der Hexactinosa von Interesse: Nach eigener Beobachtung des Typusmaterials besitzt *Mattaspongia* ausschließlich Hexactine, die in regelmäßigen vertikalen und horizontalen Zügen angeordnet sind, wobei sich die Strahlen benachbarter Hexactine überlappen (Taf. IV, Fig. 1). Wäre dieses Hexactinenskelett von einer Hülle aus sekundär ausgeschiedenem SiO_2 umgeben, ergäbe sich ein regelmäßiges, farreoides Diktyonalskelett der Hexactinosa. Da *Mattaspongia* etwa gleichzeitig mit den frühesten Hexactinosa auftritt, kommt diese Gattung als potientieller Vertreter des Adelphotaxons (Schwestergruppe) der Hexactinosa in Frage. Ebenfalls aus dem Frasné von Alberta stammt *Pelicaspongia sterrea* Rigby (1970), die Typusart der brachiospongioiden Pelicaspongiidae Rigby. Es ist der früheste Vertreter dieses Taxons, das ansonsten überwiegend aus Schichten Famenne-Alters des Canning Basins, Westaustralien (Rigby, 1986), nachgewiesen wurde. Weitere, ebenfalls die Frasné/Famenne-Grenze überschreitende Taxa sind *Teganiella* Rigby, 1979, und *Gabelia* Rigby & Murphy, 1983. Mit dem Beginn des Frasné ist eine Radiation auch der Dictyospongiidae Hall & Clarke, 1898, zu verzeichnen, die im US-Bundesstaat New York unvermittelt einsetzten. Nach Hall & Clarke (1898) fand im „Chemung" ein sprunghafter Anstieg in Zahl und Diversität der dictyospongiiden Gattungen statt, eine Tendenz die noch während des „Chemungs" kulminierte. Viele Dictyospongiidae setzten sich jedoch bis in das Mississippian hinein fort. So sind beispielsweise die von Hall & Clarke (1898) aufgeführten Gattungen *Clathrospongia* (seit dem Givet), *Dictyospongia* und *Hydriodictya* (seit dem Frasné) auch aus dem Mississippian bekannt (Rigby & Keyes, 1990; Rigby & Ausich, 1981). Die von Hall & Clarke (1898) verwendeten lithostratigraphischen Begriffe („Chemung", „Waverly", etc.) sind alte lithostratigraphische Namen, hinter denen sich diachrone Einheiten verbergen. So deckt sich das „Chemung" in Hancock (Pennsylvanian, Maryland) nur mit dem späten Frasné; in den Draper
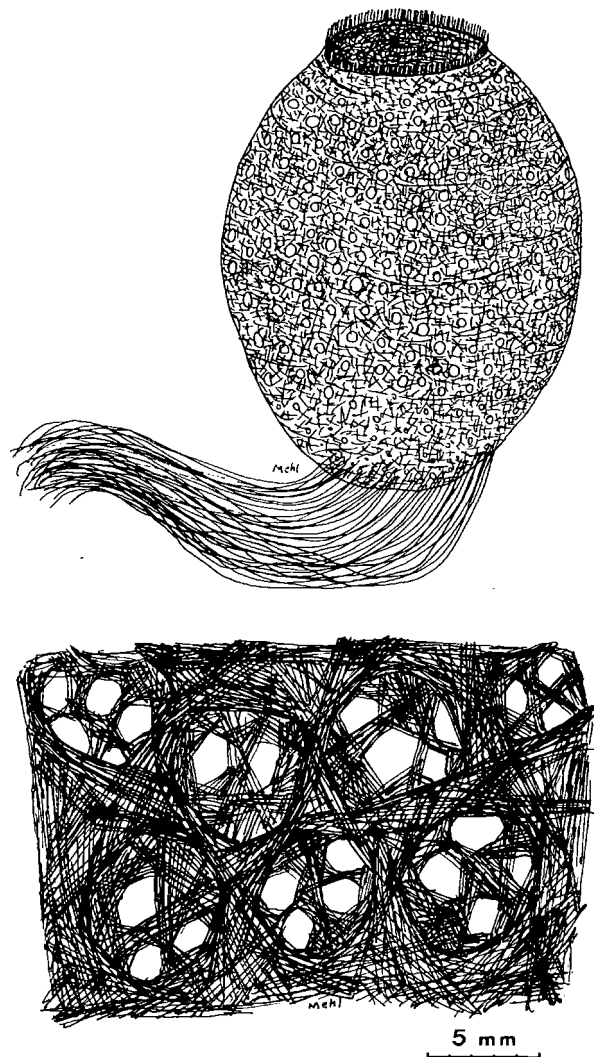

Abb. 8–9: Hexactinelliden vom Typ „Rossellimorpha" aus dem Mitteldevon von Simpson Park Range, Nevada.
8)*Teganiella ovata*; 9) *Rufuspongia triporata* mit charakteristisch doppellagiger Wand von der Oskularseite aus gesehen. Durch die großen runden inneren Öffnungen hindurch sind die kleineren Außenporen erkennbar. Dieser Schwamm zeigt die tangentiale Diactinen-Anordnung, die auch für die rezenten Rosselliidae kennzeichnend ist.

Mts., in Blue Field (West Virginia) sowie in Lackawanna und Lycoming (Pennsylvanian) dagegen mit dem Frasné bis Famenne (die stratigraphischen Daten sind dem „Oil and gas investigations chart OC-64", Oliver et al., 1988, entnommen). Es soll versucht werden, die Chemung-Fazies an ihren vielen verschiedenen Lokalitäten mit den Gattungen und Arten der Dictyospongiidae in eine chronologisch gesicherte Stratigraphie zu übersetzen, mit dem Ziel, eine aktuelle Verbrei-
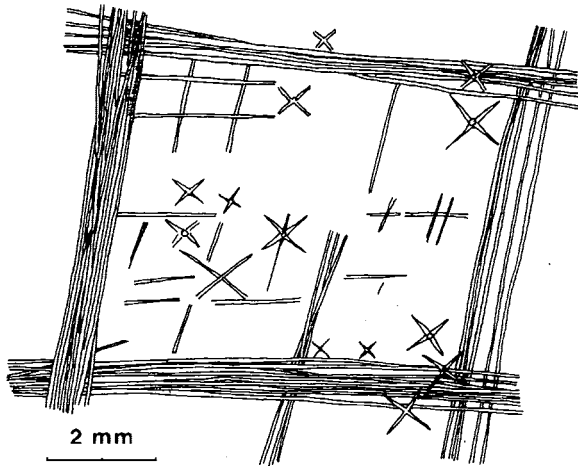
Abb. 10: Detail der Spicula-Anordnung von *Cyathophucus rhenena* (SCHLÜTER, 1892). Exemplar aus der Grube Unter-eschenbach, Bundenbacher Schiefer (Unterdevon, West-deutschland), leg. BRASSEL (SNG 218).

tungstabelle der Dictyospongiidae des Devons von New York zu erstellen. Dadurch soll die Frage geklärt werden, ob an der Frasné/Famenne-Gren-ze vielleicht tatsächlich ein Faunenschnitt der Dictyospongiidae stattgefunden haben sollte, wie von MCGHEE (1982) vertreten wird. Die bisher vorhandenen Daten widersprechen jedoch dieser Hypothese, da – soweit bekannt – die meisten Hexactinellida diese Grenze überschreiten.

3.6 Spongien des Bundenbacher Schiefers (Hunsrückschiefers)

Eine der wenigen devonischen Kieselschwamm-Lagerstätten in Europa ist der Bundenbacher Schiefer (Hunsrückschiefer, Siegen – basales Ems) des Rheinischen Schiefergebirges. Im Rah-men dieser Untersuchungen wurden Schwämme und Schwamm-ähnliche Problematika aus ver-schiedenen Hunsrückschiefer-Sammlungen unter-sucht, u.a. im Senckenberg-Museum, dem Landes-amt für Denkmalpflege in Mainz, und vielen Pri-vatsammlungen, die mir dank großzügiger Ko-operationsbereitschaft der Sammler zugänglich waren. Sie stammen aus den Gruben Eschenbach, Unter-Eschenbach und Ober-Eschenbach bei Bun-denbach. Schwämme sind im Bundenbacher Schiefer relativ selten (KUTSCHER, 1980), und bis-
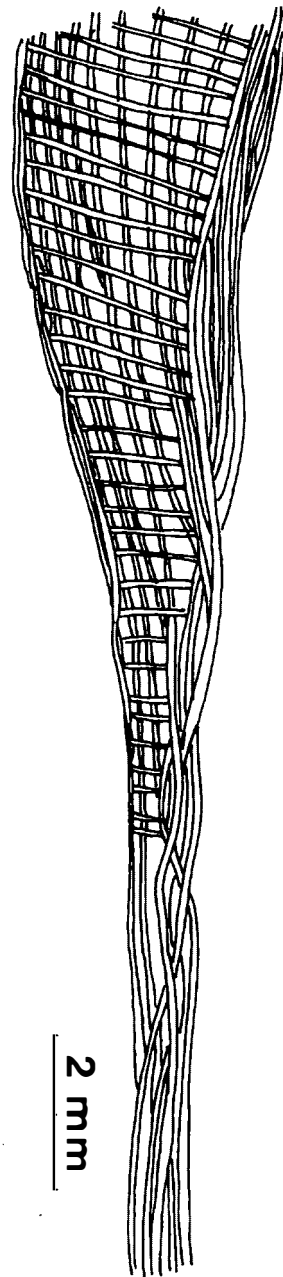

Abb. 11: Detail der Spicula-Anordnung von *Retifungus rudens* RIETSCHEL, 1970. Originalexemplar zu KOTT & WUTTKE (1987).

her wurden aus dieser Lokalität nur drei Spongien-Arten beschrieben: *Protospongia rhenana* SCHLÜ-TER, 1892, *Asteriscosella nassovica* CHRIST, 1925, und *Retifungus rudens* RIETSCHEL, 1970. Bei *Asteriscosella* handelt es sich wahrschein-lich um einen Vertreter der Demospongiae mit Affinität zur kambrischen *Choia ridley* WALCOTT, 1920. Die zwei anderen Arten sind retikulate, bis-her nur aus dem Bundenbacher Schiefer bekannte
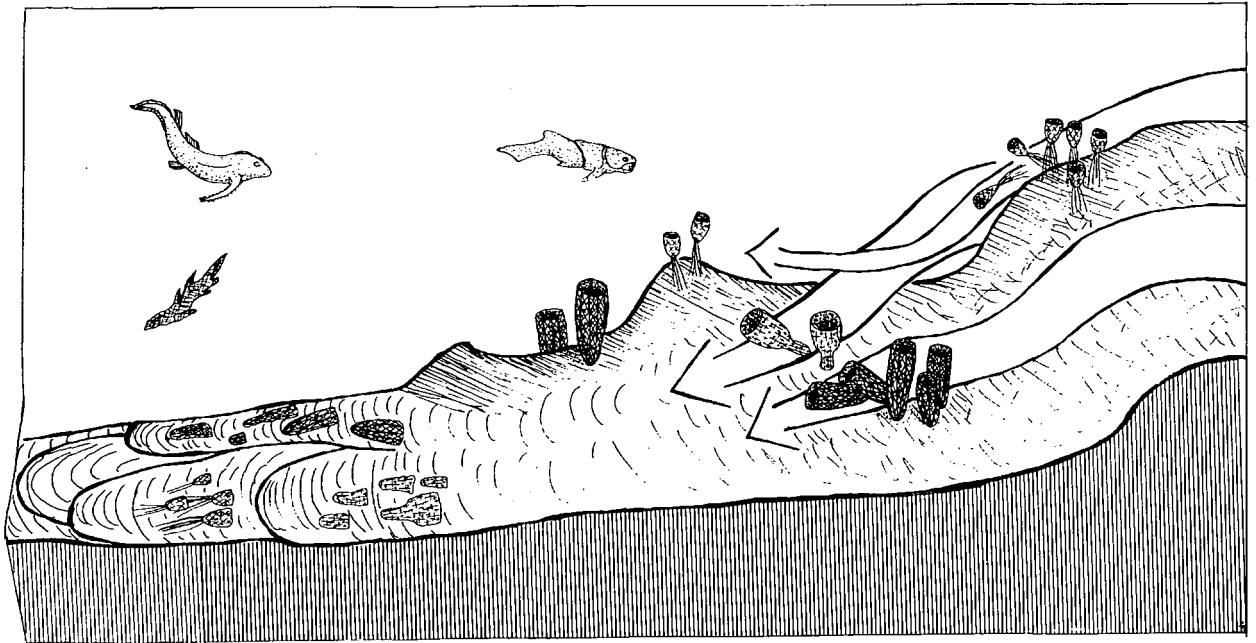
Abb. 12: Palökologisches Modell des Lebensraumes der Silur/Devon-Grenzschichten, Starvation Canyon, Nevada. Die sedimentologische Rekonstruktion basiert auf der Taphonomie der Poriferen. Demnach standen die Schwämme in diskreten Gruppierungen, nach Arten weitgehend getrennt, ähnlich wie es Rezent im Nordatlantischen Ozean zu beobachten ist. Weitere Erläuterungen im Text.

hexactinellide Arten. Im Laufe dieser Untersuchungen konnte ich noch zwei weitere, bisher unbeschriebene Demospongiae sowie einen Heteractiniden (Calcarea) (*Astraeospongium* n. sp.?) identifizieren. Diese Spongien liegen alle in zum Teil ausgezeichneter pyritischer Erhaltung vor. *Retifungus rudens* RIETSCHEL, 1970, ist von dictyospongioider Organisation, mit gewundenen Zügen aus sehr langen, ausschließlich diactinen Spicula, die sich von der Basis des seilartig gewundenen Stiels bis an den oberen Rand des Kelchs erstrecken können. Die Spicula des fragmentarisch erhaltenen Holotypus sind nach eigener Beobachtung mangelhaft erhalten und weisen an vielen Stellen kleine Brüche auf, sodaß sie aussehen wie aneinander gereihte kleine Nadeln. Dieses Erscheinungsbild ist wohl der Grund für eine Fehlinterpretation durch KOTT & WUTTKE (1987). Aufgrund von Studien des Holotypus gelangten die Autoren zu dem Schluß, daß das Schwammskelett aus vertikal/horizontal verlaufenden Skleroprotein-Fasern besteht, in denen kleine Oxen eingelagert wären. Ein weiteres, vollständigeres und außergewöhnlich gut erhaltenes Exemplar von *Retifungus rudens*, auch in der Arbeit von KOTT & WUTTKE (1987) veröffentlicht, läßt jedoch sehr instruktiv die Funktionsmorphologie der dictyospongioiden Skelettbauweise erkennen: Die sehr langen Diactine liegen in gewundenen Bündeln, die in Längs- und Querreihen miteinander verflochten sind (Abb. 11). Diese Anordnung, die nach dem Glasfaser-Prinzip eine optimale Stabilität bei gleichzeitiger Elastizität gewährleistet, ist auch für Lebensräume unter starken Strömungen ideal, wie an Standorten der rezenten *Hyalonema*, z.B. im Arktischen Ozean, beobachtet werden kann (REITNER, unveröff. Videofilm von der deutschen Arktis-Expedition 1990). Daß der Ablagerungsraum, zumindest zeitweilig, von solchen Strömungen heimgesucht wurde, ist anhand der Einregelung und Ausrichtung der Fossilien, z.B. der Arme von Ophiuren, unschwer erkennbar. Mit seinem langen, gedrehten Stiel, ähnlich dem tommotischen *Hyalosinica archaica* MEHL & REITNER (vgl. Abb. 1) oder dem rezenten *Hyalonema* GRAY war *Retifungus rudens* auch bei Strömungen aus wechselnden Richtungen optimal angepaßt. Die andere hexactinellide Art aus dem
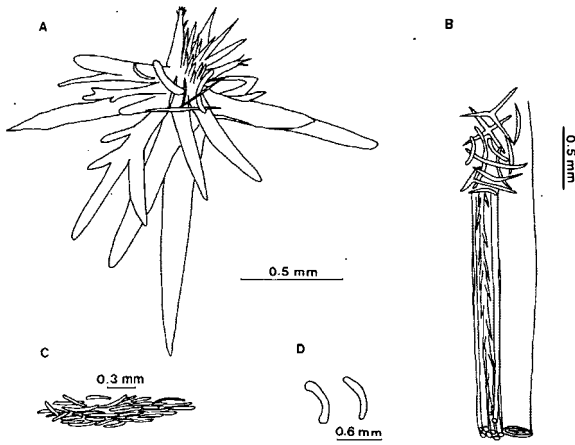
Abb. 13: Holotypus zu *Docoderma rigida* Finks, 1960, mit vielen demospongioiden Spicula. A) Dermalpentactin mit Oxen und Strongylen; B) Ausschnitt der diactinen Wurzelspicula mit Stauractinen, Oxen, Strongylen und Toxen; C) dichte Züge von Oxen und Strongylen aus dem subdermalen Bereich direkt unterhalb der Dermalpentactine; D) einzelne Strongyle aus demselben Bereich.

Bundenbacher Schiefer wurde von Schlüter (1892) als *Protospongia rhenana* beschrieben, jedoch zuletzt von Müller (1967) als „Dictyospongiide gen. inc. *rhenana* Schlüter" abgebildet. Studien umfangreichen Materials, unter anderem eines ausgezeichnet erhaltenen Exemplars aus der Sammlung Brassel (Flensburg), haben ergeben, daß diese Schwämme tatsächlich eine dictyospongioide Retikulation aufweisen. Die Art *rhenana* besitzt überwiegend gebündelte Diactine, die in vertikalen-horizontalen Längszügen geflochten, jedoch nicht gewunden sind. Außerdem besitzt der Schwamm aber noch viele kleine Triaxone (Hexactine und ?Stauractine) (Abb. 10; Taf. VII, Fig. 3). Die Spicula-Architektur stellt einen Übergang von der protospongioiden zur dictyospongioiden Organisation dar. Deshalb ist die Art *rhenana* am ehesten zur *Cyathophycus* Walcott, 1879, zu stellen, einer Gattung, die ansonsten nur aus Nordamerika bekannt ist. Dadurch wäre eine weitere Verbindung zwischen der amerikanischen und der europäischen Faunenprovinz gefunden (wie *Gabelia fascicula* aus dem Sauerland, vgl. Anhang). Ihrer Organisation nach dürfte *Cyathophycus rhenana*, ähnlich wie *Retifungus rudens*, nach dem Glasfaser-Prinzip große Stabilität besessen haben.

4. Hexactinelliden-Evolution im Jungpaläozoikum

4.1 Karbon

Reticulosa

Während des Mississippian waren die Hexactinellida sowohl auf dem Schelf, als auch in der Beckenfazies weit verbreitet. Die Reticulosa spielten weiterhin eine große Rolle. Viele Vertreter der Dictyospongiidae sind aus Ablagerungen relativ flachen Wassers deltaischer Fazies (Rigby & Ausich, 1981) bzw. sogar aus der Channelfazies des Intertidals (Rigby & Keyes, 1990) bekannt. Die Dictyospongiidae aus dem Mississippian von New York waren weiterhin in großer Formenfülle präsent. Von *Griphodictya epiphanes* Hall & Clarke, 1898, sind neben Paraclavulen auch Oxyhexaster beschrieben, weshalb die Dictyospongiidae als Gesamtgruppe zu den Hexasterophora gestellt werden. Aus ähnlich flachermarinen Environments des Mississippians von New York stammen die Titusvilliidae Caster, 1939 (Caster, 1941). Diese anscheinend lyssakinen, durch Hexactine in regulärer, kubischer Anordnung gekennzeichneten Hexactinelliden könnten, wie die Gattung *Mattaspongia* aus dem Devon (vgl. Taf. IV, Fig. 1), ebenfalls als Adelphotaxon (Schwestergruppe) der Hexactinosa in Frage kommen. Der Erhaltungszustand der bisher beschriebenen *Titusvillia*-Exemplare erlaubt darüber jedoch keine endgültige Aussage. Aus der Beckenfazies des Mississippians, beispielsweise von Afghanistan und Irland, gibt es reiche Spicula-Vergesellschaftungen verschiedenster Hexastertypen (Spirhexaster, Echinhexaster, u.a.). Schlämmproben ausgesprochener Flachwassersedimente derselben Zeit haben dagegen keine Spicula von Kieselschwämmen erbracht (Mehl & Mostler, 1993).

4.1.1 Brachiospongiidae und „Rossellimorpha"

Aus dem mittleren und späten Karbon sind die Hexactinellida als Körperfossilien relativ selten erhalten. Hierbei handelt es sich überwiegend um

Vertreter der Brachiospongioidea, die anscheinend in größeren Wassertiefen lebten (siehe unten).

Aus dem Karbon von England stammen viele Arten der vor allem hier verbreiteten *Hyalostelia* ZITTEL, 1879 (Typusart *H. smithii*), von HINDE (1887–1912) illustriert. *Hyalostelia smithii* (YOUNG & YOUNG, 1877) ist aus den frühkarbonischen Serien von Ayrshire, England (HINDE, 1888) sowie aus dem Ural (TSCHERNYSCHEW, 1898) bekannt. *Hyalostelia* wird zu den Brachiospongioidea gestellt und zeigt Affinitäten zur permischen *Stioderma* FINKS (REID, 1968; s. u.). Die aus dem Perm beschriebenen Stiodermatidae FINKS, 1960, treten bereits im Karbon auf (MOSTLER, mündl. Mitt.). Gut erhaltene Exemplare aus dem Pennsylvanian von Arkansas und Texas, die nach eigener Beobachtung einer neuen *Stioderma*-Art angehören, befinden sich derzeit noch in Bearbeitung (RIGBY, Provo, Utah). Auch die Docodermatidae FINKS, 1960, sind aller Wahrscheinlichkeit nach schon seit dem frühen Karbon vertreten. Die Dermalia von *Tholiasterella* HINDE, 1887 (in FINKS, 1960: Pl. 40, Figs. 4–7, dargestellt) aus dem Frühkarbon von Ayrshire sind denen des permischen *Docoderma rigida* FINKS, 1960, äußerst ähnlich.

Auch einige Lyssakine *incertae sedis* vom Typ „Rossellimorpha" sind aus dem späten Unterkarbon beschrieben, z.B. *Teganiella* RIGBY, 1979 (aus Kalken eines Interplattformbeckens), und *Pileospongia* RIGBY et al. (1979).

4.1.2 Amphidiscophora

Sehr selten in der gesamten fossilen Überlieferung sind eindeutige amphidiscophoride Hexactinelliden in körperlicher Erhaltung. Solche Fossilien mit Amphidisken *in situ* sind bisher nur aus dem Karbon beschrieben worden, zum einen aus dem Ural (LIBROVITCH, 1929), zum anderen aus Uruguay (KLING & REIF, 1969). Freundlicherweise wurde durch REIF die Ausleihe der Typen sowie weiteren Materials vom *locus typicus* aus Uruguay (Phosphatkonkretionen des späten Karbons aus dem Rio Negro) gestattet. Zwei Arten sind von dieser Lokalität beschrieben: *Itararella gracilis* und *Microhemidiscia ortmanni* (Taf. V, Fig. 4), letztere

ein Vertreter der seit der Spätkreide ausgestorbenen Gruppe Hemidiscaria SCHRAMMEN, 1924. Diese Schwämme sind sehr klein, nur ca. 1–2 cm in Längsrichtung, was vielleicht auf eine selektive Erhaltung der kleinen Exemplare innerhalb der Phosphatkonkretionen zurückzuführen ist. Die beiden Arten haben pentactine Dermalia, aber keine dermalen Pinule, wie es bei den rezenten Amphidiscophora häufig der Fall ist. Der Holotypus zu *Itararella gracilis* KLING & REIF zeigt Amphidisken in zwei Größenordnungen: Mesamphidisken in dermaler Position, senkrecht zur äußeren Oberfläche, sowie parenchymale Makramphidiske (35–77 μm bzw. 110–145 μm cf. KLING & REIF, 1969). Im Paratypoid Nr. 3 konnten außerdem vereinzelt Pinule in parenchymaler Position beobachtet werden. Der Holotypus zu *Microhemidiscia ortmanni* besitzt Hemidisken von anscheinend nur einer Größenordnung (115–140 μm cf. KLING & REIF, 1969), die sich häufig, aber nicht ausschließlich, in dermaler Position befinden. *Itararella gracilis* besitzt einen Wurzelschopf aus langen Ankerspicula, der weit in den Spongocoelraum hineinreicht und dort einen „Zentralkonus" bildet. Dieses Merkmal ist bei vielen rezenten Amphidiscophora, aber nur innerhalb dieser Gruppe, zu beobachten. Interessanterweise hat auch die brachiospongiide Art, *Strobilospongia tuberosa* BEECHER, 1889, einen solchen Konus, aus den Proximalenden der Wurzelspicula in den Oskularraum hineinragend, aufgrund dessen die Brachiospongiidae möglicherweise zu den Amphidiscophora zu stellen sind (siehe unten).

4.2 Perm

Hexactinellida in körperlicher Erhaltung aus dem Perm sind nicht häufig. Die einzige bisher bekannte ergiebige Lokalität ist das Perm von Texas, dessen Schwammfaunen von mehreren Autoren, z.B. GIRTY (1908), KING (1933, 1938), vor allem aber FINKS (1960) bearbeitet wurden. Das Typusmaterial zu FINKS (1960) wurde im Rahmen dieser Arbeit neu untersucht. Aus anderen Lokalitäten sind nur sporadische Funde bekannt (z.B. aus dem Perm von Südchina; RIGBY & JIASONG,

1988). Das Perm von West-Texas, gerade das Guadalupian der Glass Mts. (Beckenfazies), hat jedoch sowohl bezüglich der Diversität als auch der Individuenzahl sehr reiche Kieselschwammfaunen geliefert (siehe unten). Deshalb ist die Annahme naheliegend, daß es sich hierbei wieder um ein Fossilisations-Fenster handeln könnte, und daß die sporadische Überlieferung keinesfalls der tatsächlichen Verbreitung der Hexactinellida im Perm entspricht. Untersuchungen isolierter Schwammspicula aus verschiedenen Sedimenten bestätigen diese Vermutung. Innerhalb der Spicula-Assoziationen aus der Beckenfazies, z.B. des frühen Perms vom Vorural, ist eine deutliche Dominanz der Hexactinellida festzustellen (KOZUR & MOSTLER, 1989). Dabei ist die Diversität vor allem der Hexastertypen (z.B. die nur im Jungpaläozoikum bekannten Echin- und Spirhexaster) der Amphi- und Hemidisken auffallend groß. Ferner haben KOZUR & MOSTLER (1989: Taf. 20, Fig. 1) aus dem Perm des Vorurals ein „vom Hexactin abzuleitendes, achtstrahliges Spiculum" dokumentiert, dessen Symmetrie mit der des rezenten Discoctasters identisch ist. Der Besitz von Discoctaster-Spicula ist eine Autapomorphie der Acanthascinae IJIMA, 1898, eine Gruppe der Rossellidae sensu stricto, die ansonsten erst ab dem Lias eindeutig nachgewiesen ist (MEHL, 1992). Das Perm war eine Zeit, in der viele neue Typen rigider bzw. semirigider Skelette auftraten, die später nicht mehr verwirklicht wurden. Ein Beispiel ist das Gerüst aus Clatripentastern (MEHL & MOSTLER, 1993) in Stromatidium typicale GIRTY, 1908. Die ansonsten nur bei den lithistiden Demospongiae auftretende Gerüstbildung durch Zygose (von Hexactinen, deren aufgespaltene Strahlenenden klauenartig ineinandergreifen) ist in Irpaspongia permica MEHL & MOSTLER, 1993, realisiert.

4.2.1 Hexactinelliden aus dem Perm von West Texas

Reticulosa

Aus den permischen Glass Mountains, einer Plattformrand- bis Interplattform-Beckenfazies des Capitan Reefs in West Texas, stammt eine der interessantesten und besterhaltenen Faunen „altertümlicher" Hexactinellida. Die Spongien aus West-Texas wurden von FINKS (1960) monographisch bearbeitet, und das Typusmaterial wurde im Rahmen dieser Arbeit nochmals Gegenstand eingehender Studien. Die Hexactinelliden, darunter die „Brachiospongioidea" dominierten die Kieselschwammfauna innerhalb der Glass Mountains (Beckenfazies).

Eindeutige Reticulosa innerhalb der FINKS-Collection sind 1) Stereodictyum, bisher jüngster Vertreter der Dictyospongiide, 2) Microstaura und 3) Endoplegma.

ad 1) Stereodictyum orthoplectum FINKS, 1960, ist von typisch dictyospongiider Spikulation mit ausschließlich dünnen Diactinen in parallelen Bündeln, die von Kieselsäure umhüllt sind. Die relativ dicke Körperwand (beim Holotypus ca. 40 mm) ist nur aus solchen Diactinen-Bündeln in horizontalen und vertikalen Zügen aufgebaut. Stereodictyum tritt als erster Hexactinellider innerhalb der Schelffazies der Wolfcampian Formation (Glass Mountains) auf. Dieses Erstauftreten und das sich unmittelbar anschließende Massenvorkommen von Stereodictyum markiert das Einsetzen des Wolfcampian in West-Texas (FINKS, 1960). Die Dictyospongiidae sind im Gegensatz zu den meisten Hexactinelliden dieser Zeit nicht auf die Beckenfazies beschränkt. In West-Texas tritt Stereodictyum zugleich in Bereichen der Plattform, des Slopes und der Beckenfazies auf.

ad 2) Microstaura doliolum FINKS, 1960, besitzt kleine (nur ca. 200–500 μm lange), schlanke Hexactine in regelmäßiger kubischer Anordnung, die sehr an ein hexactinoses Diktyonalskelett erinnert. Nur die sekundäre SiO_2-Umhüllung, das rigide kieselige Basalskelett der Hexactinosa, fehlt in Microstaura. An der äußeren Oberfläche des Paratypus 127649b wurden außer pentactinen Dermalia bedornte Oxen und Strongyle beobachtet, die aber möglicherweise nicht zum Schwamm gehören. Microstaura ist eine der lyssakinen Schwammgruppen, die aufgrund der Organisation ihrer Prinzipalspicula in regelmäßigen, kubi-

schen Maschen möglicherweise dem Hexactinosa-Adelphotaxon zuzuordnen sind.

ad 3) *Endoplegma calathus* FINKS, 1960, besitzt einen Wurzelschopf und ist durch relativ große (5–10 mm), regelmäßig angeordnete Hexactine und pentactine Dermalia gekennzeichnet. Kleine Oxen kleiden sowohl die äußere Oberfläche als auch das Spongocoel aus.

4.2.2 Brachiospongioidea und „Rossellimorpha"

Zu den „Brachiospongioidea" des Perms von Texas rechnet FINKS (1960) folgende Gattungen: *Docoderma* FINKS, *Carphites* FINKS, *Acanthocoryma* FINKS, *Stioderma* FINKS, *Stromatidium* GIRTY und „Lyssacine species 3". Außerdem ist die später beschriebene *Toomeyospongia apachensis* RIGBY et al., 1982 (ebenfalls aus dem Guadalupian von West-Texas), wahrscheinlich zu den Stiodermatidae zu stellen.

Docodermatidae

Docoderma rigida ist durch sehr große (oft mehrere cm) abgewandelte Dermal-Pentactine mit wurzelähnlichen Auswüchsen und oft mit zusätzlichen Paratangentialstrahlen charakterisiert. Diese Dermalia sind über ihre „wuchernden" Auswüchse verschmolzen und bilden die rigide Außenschicht des Schwammes. Der Holotypus zeigt ferner kräftige Bündel von bis 10 mm dicken Wurzelspicula, die tief in das Spongocoel hineinragen (ähnlich dem Zentralconus von *Strobilospongia*, Brachiospongiidae, und bei vielen Amphidiscophora, s. o.). Zahlreiche, ca. 0,3–1,5 mm große fusiforme Oxen bilden dichte hypodermale Nadelzüge. Außerdem finden sich häufig „Triaene", die jedoch alle morphologischen Übergänge zu den „normalen" hexactinelliden Tauactinen zeigen.

In *Docoderma rigida* und *Docoderma papillosum* FINKS, 1960 finden sich Bündel von ca. 0,5 mm langen Oxen und Strongylen (Abb. 13).

Carphites plectus FINKS, 1960, *Carphites diabolensis* FINKS, 1960 (Taf. II, Figs. 8–9; Taf. V, Fig. 5), zeigen eine ähnliche Sklerenkonstruktion

mit großen Dermal-Pentactinen, die mit wurzelähnlichen Auswüchsen versehen sind, sowie parallel der äußeren Oberfläche prominente Züge von fusiformen Oxen und „Triaenen".

Beim Holotypus von *Acanthocoryna stauronema* FINKS, 1960, sind außerdem „Toxen" zu beobachten.

Bei den Docodermatidae finden sich interessanterweise große Mengen von Spicula, die ansonsten nur innerhalb der Demospongiae bekannt sind: Es handelt sich um fusiforme Oxen, Strongyle und „Toxen" (Abb. 13; Taf. II, Fig. 8–9; Taf. V, Fig. 5). Diese Spicula unterlagern in der Regel die großen, prominenten Dermal-Pentactine und ziehen sich hier in dichten Nadelzügen an parenchymalen Diactinen entlang. Die Regelmäßigkeit ihrer Anordnung sowie das konsequente Auftreten solcher Nadeln bei allen *Docoderma*-Arten schließen eine fremde Herkunft dieser demospongioiden Spicula aus. Ihr Vorkommen bei diesen permischen Hexactinelliden ist ein einmaliges Beispiel für eine Homoplasie zwischen Demospongiae und Hexactinellida.

Stiodermatidae

Die Typusart *Stioderma coscinum* FINKS, 1960, besitzt große, hexactine Dermalia, deren Distal- und teilweise auch Paratangentialstrahlen kugelig angeschwollen sind. Die äußere Oberfläche und das Spongocoel sind mit rigiden Schichten aus glatten, z.T. geblähten Hexactinen ausgekleidet, jedoch ohne die für *Docoderma* charakteristischen Auswüchse. Der Holotypus zu *Stioderma coscinum* zeigt einen kräftigen zentralen Wurzelschopf, der wohl ursprünglich (die Nadeln sind leider abgebrochen) tief in den Spongocoelraum hineinragte (Zentralconus!). Bei den Stiodermatidae sind, im Gegensatz zu den Docodermatidae, anscheinend demospongioide Spicula vorhanden.

Hexactinellida incertae sedis

Stromatidiidae

Die Typusart *Stromatidium typicale* GIRTY, 1909, hat ein einzigartiges Prinzip zur Bildung eines rigiden Skeletts realisiert. Durch die Bildung

horizontaler Lagen von Pentactinen mit plattenartig verzweigten Paratangentialstrahlen (=Claripentaster MEHL & MOSTLER, 1993), die wiederum mit denen benachbarter Spicula verschmelzen, entstehen rigide Gerüste. Diese Strategie unterscheidet sich markant von jeder anderen Skelettarchitektur, einschließlich jener der Brachiospongioidea, daß eine Zuordnung von *Stromatidium typicale* schwerfällt, zumal nur wenige Skelettfragmente und isolierte Spicula der Art bekannt sind.

„Rossellimorpha"

Lyssakine unsicherer Zuordnung vom Typ „Rossellimorpha" sind *Polylophidium discus* FINKS, 1960 (vom Autor zu den Teganiidae de LAUBENFELS, 1955 gestellt), sowie sämtliche der von FINKS als „Lyssacine species" Typ 1 bzw. 2 beschrifteten Hexactinelliden. *Polylophidium* mit seinen vielen Wurzelschöpfen sieht den rezenten Rosselliidae (Hexasterophora) sehr ähnlich, könnte jedoch auch den Pheronematidae (*Pheronema* LEIDY, 1868, Amphidiscophora) angehören. Leider ist es mir trotz intensiver Nachforschung nicht gelungen, irgendwelche Mikroskleren zu finden, um diese Frage zu klären.

„Pileolitidae"

Die Typusart ist *Pileolites* FINKS, 1960 (Taf. V, Fig. 6; Taf. VI, Figs. 4–5). Dieser nur wenige cm große Schwamm ist flachbödig, ohne Wurzelschopf, mit einem weiten flachen Paragaster, wo (ausführende) Kanäle in kleinen (ca. 200 μm), runden Poren münden. Innerhalb der Kanäle befinden sich große, senkrecht stehende Diactine, die aus den Poren herausragen. Die äußere Oberfläche ist als dichte Diktyonalcortex ausgebildet und mit kleinen (ca. 100 μm) Pusteln von den geschwollenen Destalstrahlen der Dermalhexactine übersät (Taf. VI, Fig. 5). Das Sklerengerüst ist äußerst unregelmäßig und besteht aus mehreren den Oscularraum überspannenden Lagen von Spicula, die keine besondere Orientierung zeigen. Innerhalb jeder dieser Lagen befinden sich bis zu 4 mm lange, horizontale Elemente, die dem Anschein nach aus jeweils zwei subparallelen, über Synapticulae zusammenhängenden Kieselsträngen bestehen. FINKS (1969: 139) hält diese für

Diactine, die über kleine silikatische Brücken (Synapticulae) verschmolzen sind. Nach eigenen Beobachtungen des Typenmaterials von *Pileolites baccatus* besitzt diese Art jedoch keine eindeutigen hexaradiaten Spicula mit rechtwinkelig zueinander stehenden Strahlen. Demzufolge finden sich im Skelett auch keine nur annähernd kubischen Maschen. Die einzelnen Elemente, aus denen sich das Gerüst zusammensetzt, sehen weder Hexactinen noch Diactinen ähnlich, dagegen erinnern sie an Tetraclone (vgl. Taf. V, Fig. 6; Taf. VI, Fig. 4).

Wahrscheinlich gehört *Pileolites* nicht zu den Hexactinellida, sondern ist ein Vertreter der Desmen-tragenden Demospongiae („Lithistida"). Die der Familie Pileolitidae später noch zugeordneten Arten, bei denen es sich mit Sicherheit um Hexactinellida handelt, z.B. *Hexactinoderma trammeri* PISERA & BODZIOCH, 1991, wären demnach anderen Taxa zuzuodnen.

5. Einige wichtige Gruppen paläozoischer Hexactinellida: ihre Phylogenie und Evolution

Reticulosa REID, 1958

Die Reticulosa sind wahrscheinlich eine sehr früh in der Erdgeschichte auftretende monophyletische Gruppe der Hexasterophora. Von *Griphodictya epiphanes* haben HALL & CLARKE (1989) Oxyhexaster beschrieben. Innerhalb der Amphidiscophora sind keine dünnwandigen Vertreter mit einer retikulären Spikulation, sondern nur relativ dickwandige, sackähnliche Formen bekannt. Rezent bevorzugen die Amphidiscophora sehr große Wassertiefen (oft 1000 m und tiefer), während die Hexasterophora generell in Wassertiefen um 200 m am häufigsten auftreten, aber auch in Tiefen von nur 20–30 m vorkommen. (REID, 1968a; Schulze 1887; MEHL, 1992). Möglicherweise leiten sich die seit dem frühen Ordovizium nachgewiesenen Hexasterophora von einer Gruppe der Reticulosa (nicht jedoch, wie früher angenommen, von den Protospongiidae, s.u.) ab. Das übereinstimmende Konstruktionsprinzip gibt

Anlaß zu der Hypothese, daß die modernen dünnwandigen, durch regelmäßige parallele horizontal-vertikale Sklerenanordnung gekennzeichneten Hexasterophorida, die Hexactinosa (Spätdevon – Rezent) und die Lychniscosa (Bajocium – Rezent), von den paläozoischen Reticulosa abzuleiten sind.

5.1 Die Protospongiidae HINDE, 1887, und die Protospongioidea FINKS, 1960

Die Frage der phylogenetischen Rolle der Protospongiidae wurde mit der phylogenetisch-systematischen Analysemethode von MEHL (1991) behandelt: Aufgrund des Fehlens des konstitutiven Merkmals, des Hexactins, kommen die Protospongiidae als Stammgruppe der „modernen" Hexactinellida, z.B. der Hexactinosa, nicht in Frage. Um die systematische Stellung der Protospongiidae innerhalb der frühpaläozoischen Hexactinellida zu klären, wurden in dieser Arbeit eingehende Studien verschiedener Typussammlungen durchgeführt. Außer dem Typusmaterial der Poriferen aus dem Burgess Shale (WALCOTT, 1920) liegen dieser Arbeit insbesondere die Originale zu den Schwämmen des Ordoviziums von Little Métis (Kanada) (DAWSON, 1888, 1889, in DAWSON & HINDE, 1888, 1889; cf. nomenclatural note CLARK, 1982) zugrunde.

Protospongia SALTER, 1864, mit der Typusart *P. fenestrata* SALTER, 1864, ist durch den ausschließlichen Besitz von Stauractinen gekennzeichnet. Diese sind in nur einer Lage im regelmäßig quadratischen Muster, meistens mehrerer Größenordnungen, organisiert (Taf. III, Fig. 3). *Diagoniella* RAUFF, 1894, mit der Typusart *Protospongia coronata* DAWSON, 1889, zeichnet sich durch Stauractine in ebenfalls regelmäßiger, jedoch diagonaler Anordnung aus (Taf. III, Fig. 1). Protospongiidae *sensu stricto* besitzen nur eine einzige Schicht von Stauractinen, die durch ihre regelmäßige horizontal-vertikale Anordnung gekennzeichnet ist. Auffällig ist ferner die generell geringe Körpergröße (nur wenige cm) dieser Schwämme. Möglicherweise waren die stauractinen Nadeln nur die Dermallagen der Protongi

idae. Die choanosomalen Spicula waren aufgrund der geringen Körpergröße dieser Schwämme als Stützelemente möglicherweise nicht erforderlich und könnten deshalb vielleicht reduziert sein. Analoge Reduktionsbeispiele sind bei vielen sogenannten „Sphinctozoen", z.B. der kretazischen *Barroisia*, zu finden (vgl. REITNER, 1992). Von MEHL (1991) wurde die Hypothese aufgestellt, daß sich bei gezielten Untersuchungen auch Protospongiide finden ließen, die Hexactine oder zumindest deutliche Abwandlungen derselben aufwiesen. Einige Protospongien der DAWSON-Sammlung besitzen tatsächlich scheinbare „Stauractine", von deren Achsenkreuzen kleine Erhöhungen, Relikte reduzierter Distalstrahlen, hervortreten. Dies trifft für die Exemplare Nr. 2.316 *Protospongia tetranema*, 2.317 *Protospongia polynema*, und 12525 *Protospongia cyathiformis* zu. Der Holotypus zu letztgenannter Art zeigt außer solchen „Distalknöpfen" auch manchmal im Achsenkreuz ein kleines rundes Loch, das als Zentralkanal eines proximalen Strahls interpretiert wird. Die Frage nach dem Ursprung des Hexactins bzw. des Stauractins wurde von MEHL (1991) und MEHL et al. (1993) ausführlich diskutiert. Es ist anzunehmen, daß das Triaxon (das reguläre Hexactin) zum Grundmuster der Hexactinellida gehört und somit in der gemeinsamen Stammart aller Hexactinelliden bereits vorhanden war. Wie von MEHL et al. (1993) festgestellt, läßt sich aufgrund des stratigraphischen Auftretens der jeweiligen Spicula nicht eindeutig entscheiden, inwiefern das Hexactin oder aber das Stauractin zuerst entwickelt wurde, da beide Nadeltypen bereits sehr früh und scheinbar gleichzeitig auftreten.

Eine Alternativhypothese, die ebenfalls in Betracht gezogen werden sollte, wäre die Ableitung aller späteren hexactinelliden Schwämme (möglicherweise aller Schwämme überhaupt) von einer planktischen Grundform, die erst zu einem späteren Zeitpunkt sessil geworden wäre (vgl. REITNER, 1992). Dieser Gedanke erscheint attraktiv, zumal die Ozeane des Proterozoikums und frühen Kambriums höchstwahrscheinlich eine flache Oxykline und somit schon in geringen Tiefen anoxische, lebensfeindliche Bedingungen aufwiesen. Eine zumindest teilweise planktische Verbreitungsstra

tegie und Lebensweise wäre daher von großem Vorteil gewesen. Larven der Hexactinellida (soweit bekannt) besitzen stauractine Larvalspicula. Es wäre denkbar, daß Stauractine-tragende Hexactinellidenlarven zu einem sehr frühen (wahrscheinlich präkambrischen) Zeitpunkt der Erdgeschichte die neue Strategie des Sessilwerdens entwickelten. Ein nur wenige Millimeter großer hexactinellider Jungschwamm könnte theoretisch die Urform von *Protospongia* gewesen sein. Diese Hypothese bleibt allerdings solange eine rein theoretische Möglichkeit, bis planktische Larven oder Larvalspicula in Sedimenten des Jungproterozoikums oder füesten Kambriums nachgewiesen sind. Die planktischen hexactinelliden Knospen, *Echidnina runnegari* BENGTSON, 1986, aus dem späten Kambrium, falls es sich hierbei wirklich um Poriferen handelt, wären der bisher einzige derartige Hinweis aus der fossilen Überlieferung.

Es steht jedoch außer Zweifel, daß die bekannten Protospongiidae des Kambriums (z.B. ?*Protospongia hicksi* aus frühkambrischen Schichten; RIGBY, 1987), keine „primitiven" Hexactinelliden (FINKS, 1970, 1983), sondern vielmehr eine abgeleitete Gruppe darstellen. Die vorliegenden Beobachtungen an den Protospongiiden der DAWSON-Sammlung bestätigen auch für die Protospongiidae die vermutete Ableitung der Stauractine vom Triaxon. Der Holotypus zur Typusart der Gattung *Diagoniella* RAUFF, 1894, *Protospongia coronata* DAWSON, 1889, ist ein kleines Exemplar mit diactinen Prostalia am Oskularrand und zentimeterlangen basalen Wurzelnadeln. In der Wand sind, außer Stauractinen nur einer Größenordnung in diagonaler Anordnung, keine weiteren Spicula erkennbar. Diese einfache Spikulation ist charakteristisch für die Gattung *Diagoniella* (vgl. *Diagoniella robisoni* RIGBY, 1978; Taf. III, Fig.1). Die Protospongiidae im engeren Sinne sind durch einfache Lagen stauractiner Spicula gekennzeichnet. Die aus dem Silur bis Frühdevon beschriebenen Arten *D. tubulare* RIGBY & HARRIS, 1979, und *D. nevadensis* RIGBY & STUART, 1988, gehören dieser Gruppe eindeutig nicht an. Für sie wird hier die Gattung *Hexatractiella* errichtet (s. Anlage). Studien einer neuen Hexactinelliden-Faunula aus

Nevada (MEHL et al., 1993) haben ergeben, daß *Hexatractiella nevadensis* (RIGBY & STUART, 1988) einen komplexeren Wandbau aufweist, mit hexactinen Prinzipalskleren in mehreren Größenordnungen, die in Längszüge stark abgewandelter Triaxone übergehen (Abb. 6–7; Taf. IV, Fig. 5). Auch der Holotypus zu *Hexatractiella tubulare* (RIGBY & HARRIS, 1979) weist nach eigener Beobachtung diesen Wandbau auf. Es ist nicht einleuchtend, wie sich diese Organisation aus der einlagigen Stauractinenschicht der Gattung *Diagoniella* ergeben könnte. *Testiispongia* RIGBY, 1983, aus dem mittelkambrischen Marjum-Kalk, House Range, Utah, ist dagegen ein Beispiel eines protospongiiden Schwammes, der außer Stauractinen auch Hexactine und weitere eindeutig vom Triaxon abgeleitete Spicula besitzt.

Viele altpaläozoische Hexactinelliden fallen in die Gruppe der Hintzespongiidae FINKS, 1983, die sowohl durch protospongiide als auch brachiospongiide Merkmale gekennzeichnet ist. Sie besitzen eine zweilagige Wand, deren Dermallage aus Hexactinen bzw. Stauractinen in regelmäßiger protospongiider Anordnung besteht. Die innere Schicht ist jedoch aus Hexactinen oder davon abgeleiteten Nadeln in irregulärer Anordnung aufgebaut: z.B. *Hintzespongia* RIGBY & GUTSCHICK, 1976; *Cyathophycus* WALCOTT, 1879; ? *Pleodioria* ÖPIK, 1961; die Teganiidae DE LAUBENFELS, 1955. Die Dierespongiidae RIGBY & GUTSCHICK, 1976, mit Wänden aus zwei Lagen jeweils parallel angeordneter Spicula, stellen eine weitere solche morphologische Übergangsgruppe dar (z. B. *Dierespongia* RIGBY & GUTSCHICK, 1976; *Kiwetinokia* WALCOTT, 1920). Diese Taxa haben eine intermediäre Stellung zwischen den durch reguläre Anordnung von Stauractinen gekennzeichneten Protospongiidae und den Brachiospongiidae mit ihren irregulär in der Körperwand verteilten Hexactinen. Aus dem Kambrium und Ordovizium sind mittlerweile viele solcher „Übergangsformen" bekannt, die sowohl regelmäßig angeordnete Hexactine als auch andere vom Hexactin abgeleitete Spicula (z.B.Stauractine) besaßen. Diese Formen sind als ein weiterer Hinweis dafür zu werten, daß die Protospongiidae *sensu stricto* als eine abgeleitete Gruppe anzusehen sind, deren

Hexactine zu Stauractinen reduziert waren. Für die Protospongiidae sowie für alle Hexactinen-tragenden, Protospongien-ähnlichen Gruppen mit Triaxonen in regelmäßiger, quadratischer Anordnung hat FINKS (1960) das Taxon „Protospongioidea" aufgestellt. Diese Gruppe ist neben den „Rossellimorpha" und den „Brachiospongioidea" FINKS, 1960, eine der großen paraphyletischen Gruppierungen, die sich durch das gesamte Paläozoikum hindurch fortsetzten.

Die nur aus dem Solnhofener Plattenkalk (Tithon, Südwestdeutschland) bekannte retikulose Art *Ammonella quadrata* WALTHER, 1904, zeigt eine protospongiide lyssakine Spikulation (Taf. IV, Figs. 3, 5). Sie war einem Flachwassermilieu, jedoch unter ruhigen Bedingungen, angepaßt, wie es bei sämtlichen Protospongiiden der Fall zu sein scheint. Bei *Ammonella quadrata* könnte es sich um ein isoliertes Vorkommen eines bis in den Jura hinein überlebenden Vertreters der Protospongiidae, oder aber um eine protospongioide Spezialentwicklung innerhalb der Hexactinosa handeln (KEUPP & MEHL, 1994).

5.2 Die Dictyospongiidae HALL, 1884, Dictyospongioidea HALL & CLARKE, 1898, (nom. transl. FINKS, 1983)

Die klassische Lokalität der paläozoischen retikulaten Hexactinelliden, der Familie Dictyospongiidae HALL, 1884, ist das Devon des US-Bundesstaates New York. Ihre Verbreitung ist über den Zeitraum vom basalen Devon bis Mississippian relativ kontinuierlich. Der Grundplan der von HALL & CLARKE (1898) monographisch vorgestellten Arten und Gattungen der Dictyospongiidae ist durch eine dünne Wandung aus Diactinen in regelmäßigen Längs- und Querreihen (Taf. V, Fig. 2) und häufig auch durch hexactine Dermalia charakterisiert. Die Dictyospongiidae *sensu stricto* traten erstmalig im Ordovizium auf. *Tiddalickia quadrata* RIGBY & WEBBY, 1988, ist durch eine äußere Schicht mit einem ausschließlich aus gebündelten Diactinen bestehenden regulären quadratischen Gitter ausgezeichnet. Die äußeren Wände dieser Schwämme zeigen somit eine dic-

tyospongiide Retikulation, ihre inneren Lagen dagegen bestehen aus kleinen Hexactinen in irregulärer Anordnung. RIGBY & WEBBY (1988) beschrieben in derselben Arbeit auch Hexactinelliden von völlig irregulärer Spikulation (*Wongaspongia*, *Liscombispongia*), deren Skleren zum Teil um runde Wandlöcher herum angeordnet sind, zugleich aber die Neigung zeigen, aus Diactinen bestehende, gebündelte Nadelzüge (Spicule Tracts) auszubilden. Die Autoren halten es für nicht ausgeschlossen, daß sich die regulären Diactinenzüge bei *Tiddalickia* von solchen Formen ableiten könnten. Es wird ansonsten meistens angenommen, daß die dictyospongiide Spicula-Organisation phylogenetisch von dem ebenfalls regelmäßigen Grundmuster der Protospongiidae abgeleitet sei (FINKS, 1970, 1983; u.a.).

Die Dictyospongiidae *sensu* HALL & CLARKE sind wahrscheinlich eine monophyletische Gruppe. Bei den „Dictyospongioidea" dagegen handelt es sich bestenfalls um eine paraphyletische Gruppierung. Die Beobachtungen an paläozoischen Hexactinelliden dieser Studie haben gezeigt, daß viele hexactinellide Gruppen die potientielle Fähigkeit besitzen, voneinander unabhängig parallele horizontal-vertikale Diactinenbündel (Spicule Tracts) zu bilden (z.B. *Sanshadictya microreticulata*, Tommot, und *Hexatractiella nevadensis*, basales Devon). Dabei leiten sich die gebündelten Nadelzüge manchmal von Dermalskleren, manchmal aber auch von den Parenchymalia ab. Zuweilen sind alle Spicula der Wand von dieser retikulaten Ausbildung betroffen (z.B. bei *Retifungus rudens* RIETCHEL, Devon, oder *Stereodictyum orthoplechtum* FINKS, Perm). Die Protospongioidea im weiteren Sinne besaßen die nötigen Eigenschaften, einen dictyospongioiden Bauplan zu entwickeln: Sie waren relativ dünnwandig, mit Stauractinen und Hexactinen in regelmäßiger vertikaler und horizontaler Anordnung. *Cyathophycus* WALCOTT, 1879, beispielsweise stellt eine morphologische Übergangsform zwischen dem protospongioiden und dem dictyospongioiden Grundmuster dar. Es kann angenommen werden, daß die dictyospongioide Organisation aus der Formenfülle der Protospongioidea (nicht aber aus den Protospongiidae *sensu stricto*)
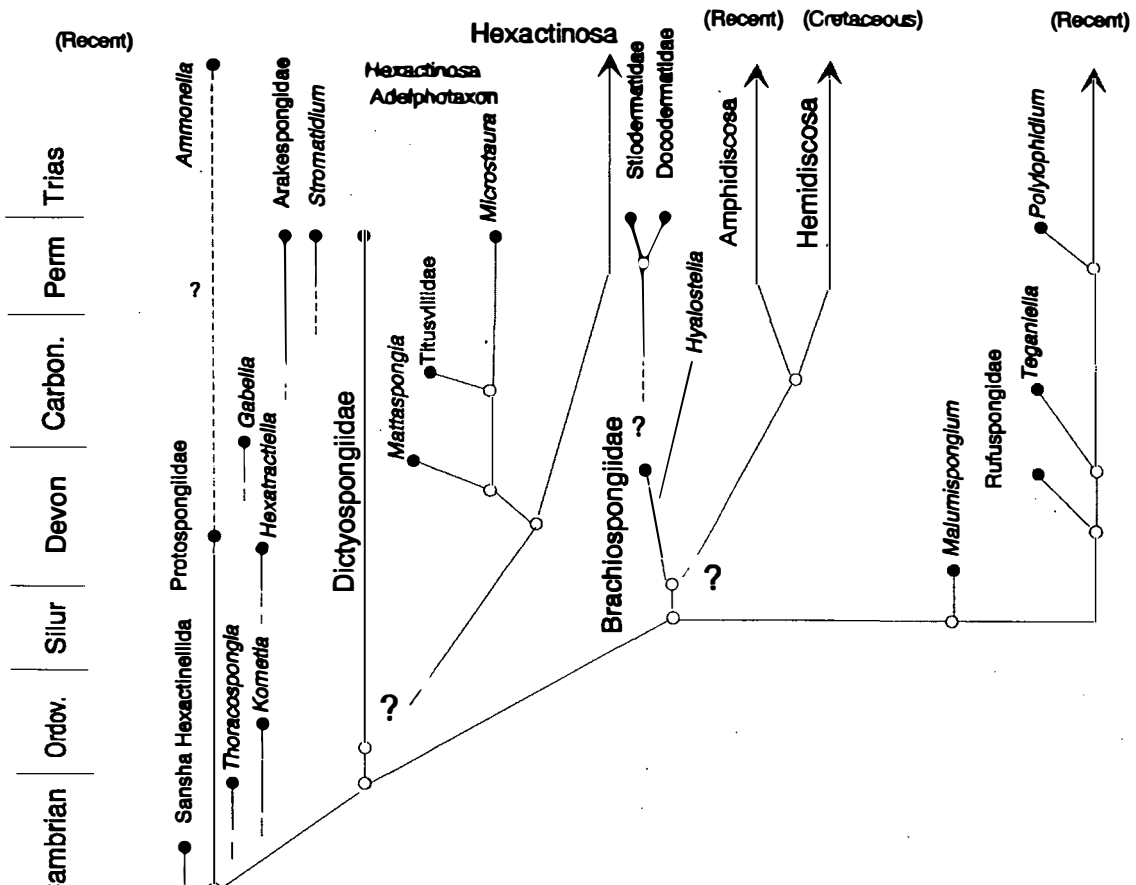
Abb. 14: Verwandtschaftsdiagramm der Hexactinelliden im Paläozoikum. Erläuterungen im Text.

entstanden ist, und zwar in mehrfach unabhängig erfolgter Parallelevolution. Für die verschiedenen Gruppen paläozoischer Hexactinelliden mit einer retikulaten Spicula-Organisation, unabhängig davon, ob nur Hexactine, Stauractine und/oder Diactine vorliegen, hat REID (1958) die Ordnung Reticulosa aufgestellt. Demnach gehören dieser Gruppe sowohl die Protospongioidea als auch die Dictyospongiidae an. REID schließt in die Reticulosa auch die karbonischen Titusvilliidae CASTER, 1939, mit ein, bei denen er von einer möglicherweise „modernen" Organisation ausgeht. Infolge REID (1958) haben sich die Reticulosa seit dem frühen Kambrium als isolierte Gruppe der Hexasterophora entwickelt und sind im späten Perm ausgestorben, ohne nähere Beziehungen zu den „modernen" Hexactinellida. Nach den hier aufgezeigten evolutiven Trends scheint aber seit (späte-

stens) dem Mittelkambrium eine Großgruppe der Hexactinellida existiert zu haben, deren Spicula nach dem Prinzip der Reticulosa in regelmäßig rektangulären, parallelen Nadelzügen angelegt waren. Diese Spicula sind grundsätzlich Triaxone, sie können aber vielerlei Abwandlungen erfahren haben, die stets aus einer Reduktion von Strahlen hervorgingen. Am häufigsten waren im Paläozoikum Nadelskelette aus Stauractinen und/oder Diactinen, meistens mit einem untergeordneten Anteil an Hexactinen. Dabei scheint die Möglichkeit, dictyospongioide Skelette mit Spicule Tracts zu entwickeln, eine kryptotypische (potientielle) Eigenschaft der Reticulosa zu sein, die immer wieder unabhängig verwirklicht wurde. Das dictyospongioide Skelett mit seinen oft gewundenen Nadelzügen aus langen Diactinen verleiht nach dem Prinzip der Glasfasertechnik dem Schwamm
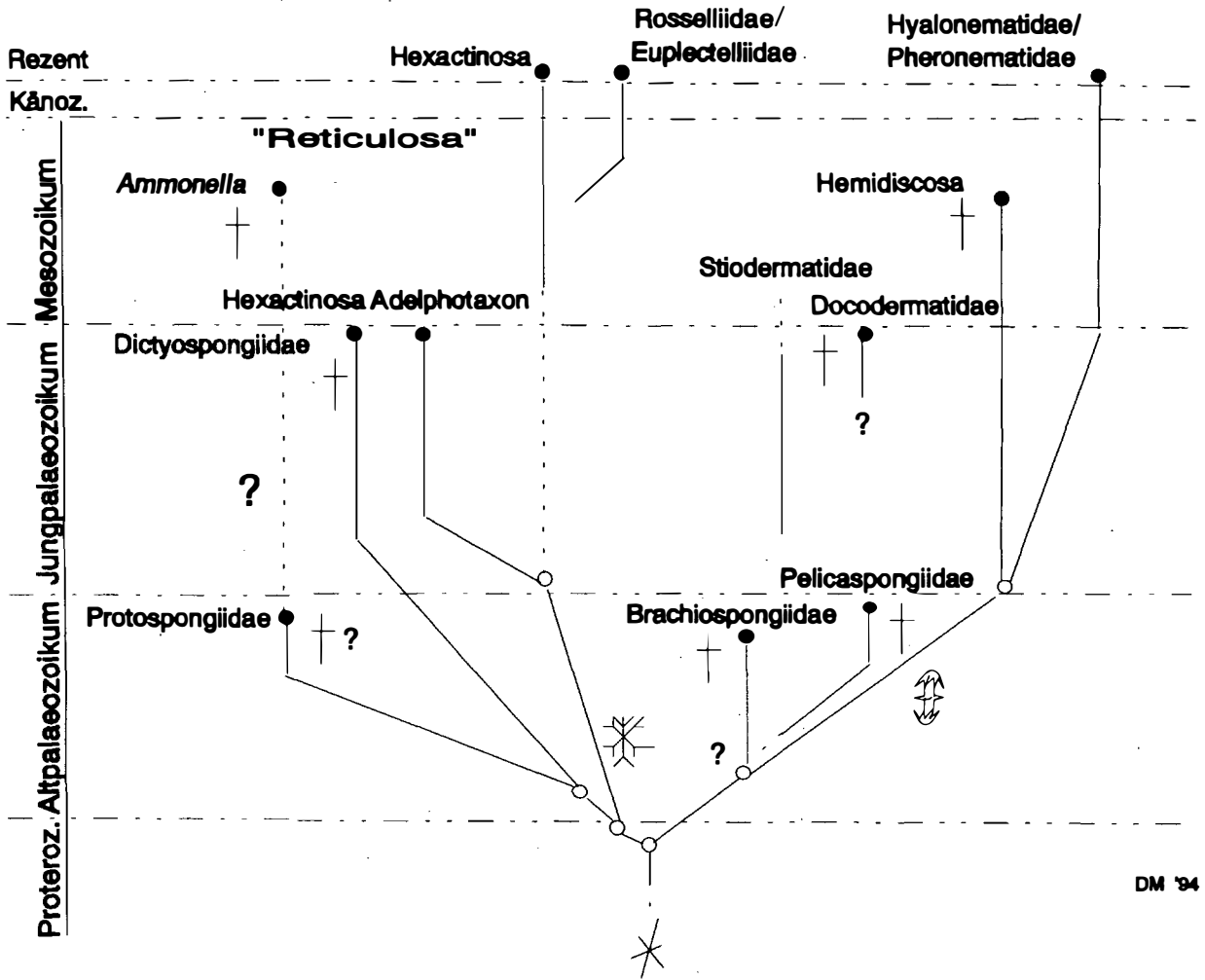
Hexasterophora | Amphidiscophora

Abb. 15: Zusammenfassung der Evolution der Hexactinellida vom Jungproterozoikum bis heute; Erläuterungen im Text.

eine große Stabilität und Elastizität zugleich (vgl. Abb. 11). Es ist eine ideale Anpassung an höher-energetische hydrodynamische Bedingungen. Das Glasfaser-Prinzip ist auch von der rezenten *Hyalonema* verwirklicht, deren Stiel aus, manch-mal meterlangen, gewundenen Spicula ein Leben unter Bedingungen starker Strömungen ermög-licht. Fossile Beispiele für diese Strategie sind *Hyalosinica archaica* (Tommot, Abb.1), *Retifungus rudens* (Frühdevon) (Abb. 11). Das Glasfaser-Prinzip ist übrigens in ähnlicher Weise auch inner-halb der Demospongiae verwirklicht, beispiels-weise bei der Art *Heliospongia excavata* GIRTY, 1908, aus den Guadalupian Mts., deren Spicule Tracts allerdings aus dichten Bündeln kleiner (ca.

0,5 mm langer) Oxen bestehen. Nach Angaben der Literatur traten dictyospongioide Hexactinel-liden häufig unter relativ flachmarinen, höher-energetischen Bedingungen auf, wo ansonsten keine Hexactinelliden leben. Die von HALL & CLARKE beschriebenen Dictyospongiidae (Devon – Mississippian, New York) stammen aus flachmari-nen, überwiegend deltaischen Sandsteinen (nach Vergleich der Lokalitäten mit Angaben von RICK-ARD & FISCHER, 1975). Auch aus intertidalen bzw. deltaischen Sedimenten des Mississippiums wur-den viele dictyospongiide Arten und Gattungen beschrieben (RIGBY & KEYES, 1990; RIGBY & AUSICH, 1981). *Stereodictyum* tritt zusammen mit *Stioderma* als einzige Vertreter der Hexactinellida

innerhalb der ansonsten nur von Demospongiae und Calcarea besiedelten Schelf- und Patch-Reef-Fazies im späten Perm von Texas auf (FINKS, 1960; vgl. auch MEHL & MOSTLER, 1993). Viele dictyospongioide Formen waren demnach speziell an die flacheren Gebiete des Littorals und Sublittorals angepaßt.

6. Die frühen Hexactinosa

Aus dem Devon sind die frühesten Vertreter einer seit dem Mesozoikum weltweit verbreiteten Gruppe der Hexasterophora, die Hexactinosa SCHRAMMEN, 1912, bekannt. Diese Schwämme zeichnen sich durch Diktyonalskelette aus, wobei ihre stets hexactinen Spicula von einer sekundären kieseligen Hülle (ein kieseliges Basalskelett) umgeben und so zu einem rigiden Skelett mit regelmäßigen kubischen Maschen verschmolzen sind. Diese diktyonalen Hexactinellida traten erstmalig etwa gleichzeitig (Frasné) an mehreren Lokalitäten auf: Heiliges-Kreuz-Gebirge, Polen (RIGBY et al., 1981); Riffe der Ardennen (von TERMIER, 1981, als „Lyssakida", *Pseudopemmatites fourmarieri* FRAIPONT, 1911, beschrieben; die Fotos in TERMIER et al., 1981: Pl. 2, zeigen jedoch eindeutig diktyonale Gitter); am Dach des ertrunkenen Atollriffs von Elbingerode, Harz (s. u.); Canning Basin, Westaustralien (*Pillaraspongia ellimberia* RIGBY, 1986). Umfassendes, zwischen 1976 und 1980 im Heiligen-Kreuz-Gebirge aufgesammeltes Material, bisher nur vorläufig durch RIGBY et al. (1981) publiziert, befindet sich derzeit in Bearbeitung (RIGBY, Provo, Utah). Diese Hexactinosa-Fauna ist nach eigener Anschauung von ausgezeichneter (kieseliger) Erhaltung und weist eine erstaunlich große Diversität auf. Die schwammführenden Bänke des Heiligen-Kreuz-Gebirges sind derzeit leider nicht aufgeschlossen, aber ein früher aufgesammeltes, gut erhaltenes Exemplar stand der Autorin für REM-Untersuchungen zur Verfügung (Taf. V, Fig. 1). Diese Spongien zeigen eindeutig rigide, dreidimensionale Diktyonalskelette aus verschmolzenen Hexactinen. Unter ihnen befinden sich viele Exemplare, die „craticulariide" (REID, 1958–1964) und tretodictyide Kanal-

systeme („*Schizorhysis*" cf. IJIMA, 1927) mit Epi- und Aporhysis zeigen (Poren der äußeren Oberfläche und der Oscularwand). Die Hexactine der Diktyonalskelette haben zum Teil verdickte Kreuzungsknoten, zeigen jedoch erwartungsgemäß keine Lychniske. Es sind durchaus „moderne" Organisationstypen, wie wir sie auch im Mesozoikum und Rezent finden. PISERA & BODZIOCH (1991) haben vorgeschlagen, daß die Diktyonalskelette der devonischen Hexactinellida und die der mesozoisch-rezenten Hexactinosa konvergent entstanden seien. Trotz des Problems des noch fehlenden Nachweises der Hexactinosa aus dem Jungpaläozoikum möchte ich mich aufgrund eigener Beobachtungen dieser Hypothese einer Homoplasie nicht anschließen. Die diktyonalen Hexactinelliden des Heiligen-Kreuz-Gebirges sind keine „einfachen" regulären, netzartigen Formen (PISERA & BODZIOCH, 1991), sondern sie zeigen in ihrer Skelettarchitektur die ganze Bandbreite der mesozoischen Hexactinosa. Aus meiner Sicht ist der fehlende Nachweis der Hexactinosa aus dem Jungpaläozoikum eine Dokumentationslücke. Die Hexactinellida dieser Zeit sind hauptsächlich aus der vor allem durch lyssakine Formen gekennzeichneten Beckenfazies bekannt (vgl. MEHL & MOSTLER, 1993). Eine weitere interessante Spongiolith-Fazies des Frasnés befindet sich im Hangenden des Atollstadiums (Givet) im Elbingeröder Komplex, Harz. Die generelle sedimentäre Entwicklung von Riffen über Stromatolithe, laminierte Zebrakalke und Stromatactis-Kalke zu „dunklen Schlammkalken" wird von WELLER (1989a; 1991; u.a.) als transgressive Abfolge interpretiert. Die laminierten Mikrobialithe (sogenannte „Mud Mounds" cf. WELLER, 1989a, 1989b; u.a.) enthalten die möglicherweise bisher ältesten Reste von Diktyonalgerüsten hexactinoser Schwämme. Durch WELLER (Greifswald) wurden mir freundlicherweise Handstücke und Dünnschliffe zur Verfügung gestellt. Im Dünnschliff lassen sich gelegentlich Relikte diktyonaler Skelette als kubische Maschen erkennen (Taf. V, Fig. 3). Außer diesen Diktyonalgerüsten finden sich isolierte Stierauctine und andere Triaxone, die jedoch möglicherweise von lyssakinen Hexactinelliden stammen. Die Gerüste liegen in sehr

schlechter, kalzitischer Erhaltung vor, und wahrscheinlich ist ein großer Teil der ursprünglich vorhandenen Schwammskelette bereits weggelöst. Die Abfolge zeigt charakteristische Mikrobialith-Strukturen (vgl. REITNER, 1993): Die Poriferen sind häufig von laminierten Krusten umgeben. Das Sediment besteht aus laminierten hellen Kalken, in die auch rote Lagen eingeschaltet sind, welche auf die Aktivität von Fe-Bakterien hindeuten. Außerdem sieht man im Dünnschliff häufige „Stylolithen", die auf intensive frühdiagenetische Lösung durch die Elektronenwanderung bei unterschiedlichen Redox-Potientialen an der Basis mikrobieller Filme hindeuten. Der Elbingeröder Mikrobialith liefert ein klassisches Beispiel für die konservative, im Laufe der Erdgeschichte bis heute immer wieder zu beobachtende, enge Vergesellschaftung mikrobieller Krusten mit Schwämmen (REITNER, 1993).

Das plötzliche Auftreten der Hexactinosa an vielen Lokalitäten im Frasné und ihr fehlender Nachweis zwischen dem späten Devon und der Mitteltrias gibt Rätsel auf. Zumindest eine hexactinose Art, *Pillarspongia ellimberia* aus dem Canning Basin, ist außerdem, wenn auch selten, im Windjana-Kalk, Famenne-Alter, gefunden worden (RIGBY, 1986). Häufig sind die paläozoischen Hexactinosa im Zusammenhang mit einer Riffentwicklung zu finden (z.B. Ardennen, Elbingerode, Canning Basin), und ihre bevorzugten Lebensräume scheinen in zwar ruhigen Environments, jedoch nicht allzu großen Wassertiefen gewesen zu sein. Möglicherweise haben die Hexactinosa während des Karbons und des Perms in kryptischen Nischen gelebt, ähnlich der heute noch überdauernden Gemeinschaften coralliner Schwämme aus der Kreidezeit (vgl. REITNER, 1992).

6.1 *Brachiospongia* MARSH, 1867, die Brachiospongiidae BEECHER, 1889, und die „Brachiospongioidea" FINKS, 1960

Die Gattung *Brachiospongia* MARSH, 1867, ist im wesentlichen durch ihre auffälligen äußeren Merkmale begründet: tassen- oder vasenförmig,

mit 8 bis 12 randlichen, armähnlichen Vorstülpungen, die nach unten abgebogen sind und bis zur Basis des Schwammkörpers herunterragen (Taf. VI, Fig 1). Der große Oskularraum setzt sich in diese „Arme" hinein fort, die dadurch hohl, jedoch an ihren Distalenden geschlossen sind. BEECHER (1889) hat die Diagnose erweitert, um insbesondere die Spikulation der Typusart *Brachiospongia digitata* OWEN, 1858, zu erfassen: Die Außenseite der ca. 1–2 cm dicken Körperwand ist von einem sehr feinen Netz aus Stauractinen in quadratischen Maschen überzogen. Die Hypodermalia sind bis mehrere mm große Hexactine mit kugelig geschwollenen Distal- und Paratangentialstrahlen sowie sehr langen, weit in die Körperwand hineinragenden Proximalstrahlen. Die darunter liegenden Parenchymalia sind Hexactine in verschiedenen Größen und unregelmäßiger Verteilung. Außerdem hat BEECHER (1889) an der Außenseite gut erhaltener Exemplare kleine Erhöhungen (Mammellonen) beobachtet. Regelmäßig auftretende stabähnliche Diactine, die in unmittelbarer Fortsetzung der Dermalia im Sediment steckten, wurden von BEECHER (1889) als möglicherweise zum Schwamm gehörige Prostalia interpretiert (jedoch hat er diese in seiner zeichnerischen Rekonstruktion von *Brachiospongia* weggelassen). Dermale Poren wurden nicht beobachtet, aber zum Oskulum hin mündende unregelmäßige, runde bis ovale Öffnungen sind vorhanden.

Als weitere Gattung der Brachiospongiidae wurde *Strobilospongia* (Typusart *S. tuberosa* BEECHER, 1889) beschrieben, deren Spikulation der Autor als sehr ähnlich der bei *Brachiospongia* beobachteten bezeichnete. Reste sowohl des für *Brachiospongia* typischen feinen dermalen Stauractinen-Netzes, als auch der groben, geschwollenen Hypodermalia, will BEECHER (1889) bei *Strobilospongia* erkannt haben. Er stellte die beiden Gattungen deshalb in seine Familie Brachiospongiidae. *Strobilospongia* ist jedoch durch eine weitere Eigenschaft ausgezeichnet, die bei *Brachiospongia* nicht beobachtet wird: den Besitz eines 1–2 cm dicken, möglicherweise leicht gewundenen (dies läßt sich anhand der abgebildeten Stücke nicht entscheiden) Wurzelschopfes,

der weit in das Osculum des tulpenförmigen Schwammkörpers hineinragt und dort, auf etwa halber Höhe „verankert", einen Zentralkonus bildet. Dieses Merkmal ist ansonsten nur von Vertretern der Amphidiscophora bekannt, z.B. den Gattungen *Semperella* GRAY, 1868, und *Hyalonema* GRAY, 1832 (Kreide – Rezent), wobei letztere auch ihrer Körperform nach mit *Strobilospongia* große Ähnlichkeit zeigt, (vgl. z.B. *Hyalonema depressa* SCHULZE, 1887: Pl. 35, Figs. 1, 2). Das von BEECHER (1889) sowohl von *Brachiospongia* als auch *Strobilospongia* beschriebene, die äußere Oberfläche überziehende quadratisch-maschige Netz aus sehr feinen Dermalia ist auch von vielen rezenten Amphidiscophora bekannt: *Hyalonema* GRAY, *Poliopogon* THOMSON, *Semperella* GRAY. Teilweise handelt es sich hierbei um pentactine und nicht um stauractine Dermalia, was bei Fossilien in kalkiger Erhaltung jedoch kaum unterscheidbar wäre. Wir finden innerhalb der Amphidiscophora keine dünnwandigen, retikulaten Formen, sondern immer nur Schwämme von dickwandigem, sackförmigem Habitus (der allerdings auch bei den Hexasterophora der Gruppe Rosselliidae vorkommt). BEECHER (1889) nimmt für die Brachiospongiiden-führenden Schichten an, daß es sich um Tiefwassersedimente handelt. Rezentbeobachtungen zufolge bevorzugen die Amphidiscophora unter den Hexactinelliden die größten Wassertiefen (häufig 1000 m und mehr, REITNER, pers. Mitt.), während die Hexasterophora gelegentlich auch in relativ flachem Wasser anzutreffen sind (MEHL, 1992). Aus diesen Gründen schlage ich vor (mit Vorbehalt, aufgrund des bisher fehlenden Nachweises von Amphidisken), die Brachiospongiidae zunächst den Amphidiscophora zuzuordnen.

Das Taxon „Brachiospongioidea" umfaßt nach der Diagnose von FINKS (1960: 115): „vasenförmige Spongien mit großen runden Wandlöchern; spezialisierte Dermalschicht aus großen Spicula, normalerweise Pentactine, mit charakteristischen Auswüchsen der distalen Oberflächen, in einigen Arten mit extra paratangentialen Strahlen; ein supradermales, quadratisches Netzwerk aus kleinen Pentactinen oder Stauractinen ist oft vorhanden; innere Spicula ohne einheitliche Orientierung."

Diese Diagnose entspricht weitestgehend den Angaben BEECHERS (1889, siehe oben) über die Spikulation der Brachiospongiidae. Die eingesetzten Merkmale gehören sehr wahrscheinlich auch zum Grundmuster der Amphidiscophora. Ihr Auftreten innerhalb dieser Gruppe ist daher als plesiomorph zu werten. Bei den „Brachiospongioidea" dürfte es sich demnach um eine paraphyletische Gruppierung innerhalb der Amphidiscophora handeln. Da verdickte Dermalspicula zudem ein äußerst konvergenzanfälliges Merkmal ist, das innerhalb der Hexactinellida mehrfach entstanden ist, könnten die „Brachiospongioidea" vielleicht sogar ein polyphyletisches Taxon sein. Nach eigenem Studium des Typusmaterials zu den von FINKS (1960) publizierten permischen Kieselschwämmen aus Texas stimmt die Autorin der Klassifikation vieler seiner Taxa, z.B. der Docodermatidae und Stiodermatidae, als „Brachiospongioidea" (als Morphotyp) zu. Ob es sich bei diesen Gruppen auch um Amphidiscophora handelt ist unsicher, jedenfalls ließen sich trotz intensiver Suche keine Amphidisken entdecken, was jedoch angesichts des geringen Erhaltungspotentials hexactinellider Mikroskleren *in situ* nicht verwunderlich ist. In jüngerer Zeit wurden allerdings viele Taxa allein aufgrund der Körperform und ihrer irregulären Spikulation den „Brachiospongioidea" zugeordnet, obwohl bei ihnen eine charakteristische Außenschicht aus großen, abgewandelten Dermalspicula nicht beobachtet wurde. So ist beispielsweise die systematische Stellung der aus dem Karbon bekannten Gattung *Hyalostelia* ZITTEL, 1879, nicht befriedigend geklärt. Die Typusart *Acanthaspongia smithii* YOUNG & YOUNG, 1877, ist hauptsächlich aufgrund isolierter, aus langen Ankerspicula aufgebauter Wurzelschöpfe bekannt. Über den Charakter der Dermalia und Parenchymalia von *Hyalostelia* herrscht Unklarheit (in YOUNG & YOUNG, 1877: pl. 14, sind auch Polyactine abgebildet, die jedoch wahrscheinlich nicht zur selben Art gehören; vgl. HINDE, 1887–1912). Vor allem aufgrund der auffälligen Ähnlichkeit dieser Wurzelspicula mit denen der rezenten Gattung *Hyalonema* wird *Acanthaspongia* von CARTER (1877) als ein naher Verwandter dieses amphidiscophoriden Taxons angesehen.

Die Revision der Typen unter Einbeziehung neuen Materials brachte REID (1968b) zu der Ansicht, daß *Hyalostelia* zwar vergrößerte Hypodermalia besitzt, daß aber kein autodermales Netz, wie für die Brachiospongiidae charakteristisch, existiert (was jedoch auch eine Frage mangelhafter Erhaltung sein könnte). REID (1968b) stellte *Hyalostelia* zu den Brachiospongioidea und zwar in unmittelbare Nähe der spätpermischen *Stioderma* FINKS, 1960, eine Auffassung, der sich die Autorin nach eigenen Beobachtungen an *Stioderma coscinum* FINKS, 1960, und *Hyalostelia* div. sp. (Natural History Museum, London) anschließen möchte.

7. Phylogenie und Evolutionsökologie der Hexactinellida im Paläozoikum: Ergebnisse und Diskussion

Die seit dem Jungproterozoikum bekannten Hexactinellida sind die älteste mit Sicherheit nachgewiesene, heute noch lebende Metazoengruppe. Bereits im Tommotian treten die Hexactinellida, deren Entstehung weiter im Präkambrium zurückliegen dürfte, in großer Formenfülle auf. Die Hexactinellida sind nicht nur eine sehr alte, sondern auch eine ultra-konservative Gruppe. Alle Großgruppen, außer den Lychniscosa, sind schon aus dem frühen Paläozoikum nachgewiesen. Dennoch lassen sich die paläozoischen Hexactinelliden, von wenigen Ausnahmen abgesehen, in die Rezentsystematik nur mit großer Unsicherheit einhängen. Dies liegt zum einen an der mangelhaften Erhaltung dieser fossilen Spongien, deren Mikrosklaren, wichtigstes Merkmal für die systematische Klassifikation, nur ausnahmsweise *in situ* gefunden werden. Zum anderen unterscheidet sich die Skelettarchitektur der meisten paläozoischen Hexactinelliden derart von jener der mesozoischen und rezenten Gruppen, daß gesicherte systematische Vergleiche in der Regel kaum möglich sind. Der Sachverhalt erscheint zunächst widersprüchlich: Obwohl die Hexactinellida eine sehr konservative Gruppe sind, lassen sich ihre paläozoischen Vertreter mit denen des Mesozoikums bis Rezent nur schwer vergleichen. Dies erklärt sich aber durch die Tatsache, daß viele Gruppen der Hexactinellida (beispielsweise die Hexactinosa) über lange Zeiträume während des Jungpaläozoikums anscheinend in kryptischen bzw. fossil nicht überlieferten Habitaten, z.B. der abyssalen Zone, siedelten. Anders angepaßte Formen (z.B. die Dictyospongiidae) konnten sich währenddessen in flacheren Schelfgebieten einnischen, wo ihr Erhaltungspotential höher war. Dadurch erklärt sich auch das durch die Erdgeschichte hindurch scheinbar sporadische Auftreten der Hexactinellida. Perioden des fast völligen Fehlens körperlich erhaltener Hexactinelliden wechseln sich mit Phasen anscheinend unvermittelter radiativer Verbreitung ab. Die Berücksichtigung isolierter Spicula aus Sedimenten, insbesondere nicht-turbiditischer Beckenablagerungen, wie es in dieser Arbeit versucht wurde, zeigt jedoch, daß dieser erste Eindruck nicht haltbar ist. Im Gegensatz zum sporadischen „Massenauftreten" scheint die Evolution der Hexactinelliden innerhalb der bereits im frühen Paläozoikum auftretenden Adelphotaxa: Hexasterophora und Amphidiscophora (Abb. 14, 15) sehr kontinuierlich abgelaufen zu sein.

Die paläozoische Großgruppe der Reticulosa gehört wahrscheinlich in die phyletische Linie der seit dem Frühordovizium nachgewiesenen Hexasterophora. Zu den Reticulosa sind außer den **Dictyospongiidae** *sensu* HALL & CLARKE wahrscheinlich auch die seit dem Devon (Frasné) bekannten **Hexactinosa** zu stellen. Morphologische „Übergangsformen" wie *Mattaspongia, Hintzespongia, Cyathophycus, Dierespongia,* u.a. deuten auf phylogenetische Beziehungen zwischen den Reticulosa und den Hexactinosa hin. Die kambrischen Protospongiidae *sensu stricto* sind ein früher, noch im Altpaläozoikum erloschener Seitenzweig der Reticulosa. Die Vertreter dieser Gruppe waren durch extrem dünnwandige Körper mit ausschließlich stauractinen Spicula in regelmäßiger quadratischer Anordnung gekennzeichnet. Als Paradigma für das Grundmuster der Reticulosa müssen jedoch eher die Gattungen *Mattaspongia* (Devon) oder *Microstaura* (Perm) mit

ihren nicht verschmolzenen Hexactinen in regelmäßiger kubischer Anordnung gelten. Überraschenderweise ist jetzt eine lyssakin-retikulate hexactinellide Art aus dem Mesozoikum bekannt geworden. *Ammonella quadrata* WALTHER, 1904, aus dem Solnhofener Plattenkalk (Tithon, Südwestdeutschland) bekannt, wurde ursprünglich als diktyonale Form der Euretidae beschrieben. Neuerliche Untersuchungen haben jedoch ergeben, daß es sich hierbei um einen Lyssakinen mit großer Affinität zu den Protospongiidae handelt (KEUPP & MEHL, 1994). Es ist demnach denkbar, daß diese altpaläozoische Gruppe, die an nichtturbulente Flachwasserbiotope adaptiert war, die Perm-/Trias-Grenze überlebten. Aus dem Grundmuster der Hexactinosa-Schwestergruppe (*Mattaspongia*-Spikulation) konnten sich durch Strahlenreduktion innerhalb bestimmter Körperlagen (dermal bzw. parenchymal) immer wieder Gruppen mit einer retikulaten Spikulation, ähnlich den Dictyospongiidae, entwickeln. Die dictyospongioide Retikulation scheint eine spezielle Anpassung an höherenergetische Bedingungen in geringeren Wassertiefen zu sein. Die dictyospongiide Skelettarchitektur mit ihren parallelen, horizontal-vertikal verlaufenden, gewundenen Spicula-Zügen (Züge von Diactinen) funktioniert nach dem Glasfaser-Prinzip: Sie besitzt die bei größerer Wasserenergie wechselnden Strömungsrichtungen usw. erforderlichen Eigenschaften von Stabilität bei gleichzeitiger Elastizität. Dictyospongioide Hexactinelliden sind sogar in intertidalen Sandsteinen des Mississippium gefunden worden (RIGBY & KEYES, 1990).

Die Schwestergruppe der Hexasterophora, die **Amphidiscophora**, sind erst aus dem späten Silur eindeutig nachgewiesen, wir können aber nach dem Prinzip des *terminus post quem non* von der gleichzeitigen Existenz der beiden Adelphotaxa ausgehen. Demnach müssen wir mit dem Vorhandensein der Amphidiscophora seit spätestens dem frühen Ordovizium rechnen. Es ist jedoch möglich, daß Vertreter dieser Gruppe das Merkmal Amphidisken erst zu einem späteren Zeitpunkt entwickelten, und daß deshalb dieser Spiculatyp trotz intensiver Nachforschungen an ordovizi-

schen Sedimenten nicht gefunden wurden. Die ebenfalls ab dem Ordovizium auftretende paläozoische Gruppe der Brachiospongiidae gehört möglicherweise in das Taxon Amphidiscophora. Zumindest die innerhalb der Brachiospongiidae *Brachiospongia* wahrscheinlich nächststehende Gattung *Strobilospongia* zeigt große Ähnlichkeit mit fossilen (z.B. *Itararella*, *Microhemidiscia*) sowie mesozoisch-rezenten (z.B. *Hyalonema*, *Semperella*) Amphidiscophora. Obwohl bei den Brachiospongiidae noch keine Amphidisken *in situ* nachgewiesen sind (in der fossilen Überlieferung überhaupt eine große Seltenheit), geben die allgemeine Morphologie und die Skelettarchitektur sowie die Palökologie Hinweise auf eine amphidiscophoride Affinität dieser Gruppe. Bei den spätpermischen „Brachiospongioidea", z.B. den Docodermatidae und Stiodermatidae, handelt es sich den Dermalskleren und dem auf die Beckenfazies beschränkten Auftreten nach zu urteilen wahrscheinlich auch um Amphidiscophora. Das feine retikuläre Netz über große Hypodermalia ist jedoch ein plesiomorphes, bereits im Ordovizium bei *Strobilospongia* auftretendes Merkmal dieser Gruppe. Deshalb sind die „Brachiospongioidea" als eine paraphyletische Gruppierung innerhalb der Amphidiscophora anzusehen. Da die dictyospongiide Spikulation allem Anschein nach aus dem reticulosen Grundmuster mehrfach konvergent entstanden ist, sind die „Dictyospongioidea" eine polyphyletische Gruppierung innerhalb der Hexasterophora.

Ein seit dem frühen Kambrium bis heute durchgehender, nicht weiter auflösbarer „Grundstock" konservativer Hexactinelliden wird hier als „Rossellimorpha" bezeichnet. Es handelt sich hierbei um eine rein morphologische Bezeichnung für eine bestenfalls paraphyletische, eventuell sogar polyphyletische Gruppierung, die im ausschließlich beschreibend-morphologischen, nicht aber im taxonomischen Sinne verwendet wird. Die „Rossellimorpha" sind lyssakine, relativ dickwandige, sackförmige Hexactinelliden, deren Spicula, überwiegend zu Diactinen reduziert, tangential um Poren der Wand angeordnet sind (vgl. Abb. 9). Paläozoische Beispiele dieses nach der rezenten *Rossella* CARTER, 1872, benannten Mor-

photyps sind: *Stephenospongia* RIGBY, 1986a (Mittelkambrium); *Wongaspongia* RIGBY & WEBBY, 1988 (Ordovizium); *Malumispongia* RIGBY, 1967 (Silur); *Rufuspongia* RIGBY & MEHL, in Druck (Devon); *Pileospongia* RIGBY et al., 1979 (Karbon); *Polylophidium* FINKS, 1960 (Perm). „Rossellimorpha" sind generell Schwämme der Beckenfazies, doch finden sich hier auch Formen, die in flacheren, jedoch immer sehr ruhigen Environments (unterhalb der Sturmwellenbasis) siedelten.

Seit dem Kambrium sind die Hexactinellida stets in Ruhigwasser-Paläoenvironments, häufig solchen der Slope- und Beckenfazies, zu finden. Im Laufe der Erdgeschichte gab es jedoch immer wieder Zeiten, in denen spezialisierte Teilgruppen zusätzlich verstärkt die flacheren Schelfgebiete besiedelten. Solche Phasen der Erschließung neuer ökologischer Zonen gehen mit einer phylogenetischen Radiation, mit Neu-Einnischungen und der daran geknüpften vielseitigen Entwicklung bestimmter Merkmalkomplexe einher. Aus dem genetischen Potiential eines Grundplans ist es in paralleler Evolution wiederholt zu ähnlichen Entwicklungen (Homoplasien) gekommen. Ein Beispiel dafür ist die Tendenz innerhalb der Reticulosa, unter relativen Flachwasserbedingungen immer wieder dictyospongioide Spiculazüge hervorzubringen. Die Hauptphase einer solchen verstärkten paläozoischen Schelfbesiedelung, die für bestimmte Hexactinelliden-Gruppen die Chance der fossilen Überlieferung in einzelnen „Erhaltungsfenstern" ermöglicht, stellt weltweit die Periode vom basalen Oberdevon (Frasné) bis Ende des Mississippians dar. Phasen, in denen die Hexactinelliden weitgehend für die Paläontologie „unsichtbar" blieben, reichen vom Oberkambrium bis ins Mitteldevon und vom Oberkarbon bis in die Mitteltrias. Wenn es gelingt, ihre Ökozonierung während dieser Zeiten, insbesondere des Ordoviziums, zu erfassen, scheinen die Poriferen jedoch sehr gute palökologische Anzeiger zu sein (vgl. die Spicula-Verteilung aus dem Frühordovizium der San Juan Formation, bzw. der aus dem Geschiebe von Sylt).

Zeiten einer intensiven radiativen Evolution innerhalb der Hexactinellida korrespondieren mit ihrer vorübergehenden Platznahme in Flachschelfarealen mit guter Wasserzirkulation: Dies war anscheinend im Mittelkambrium der Fall, im basalen Oberdevon (Frasné) und im basale Oberperm (Guadalupian). Es handelt sich hierbei um „Experimentierfelder", innerhalb derer verstärkt neue Strategien verwirklicht wurden, von denen sich allerdings nur die wenigsten auf längere Sicht durchsetzen konnten. Die fossil überlieferten Hexactinellida des Mittelkambriums stammen hauptsächlich aus distalen Turbidit- bzw. Tempestitablagerungen (z.B. Burgess und Wheeler Shales), deren Event-Charakter nicht zuletzt durch die jeweilige Verteilung der Spongien angezeigt ist (vgl. MEHL et al., 1993). Dasselbe scheint für die frühkambrischen Fossilisationsfenster von Chengjiang und Sansha zuzutreffen (ERDTMANN et al., 1994).

Aus unbekannten Gründen muß im Kambrium ein Selektionsdruck in Richtung starke äußere Bepanzerung bestanden haben. Dies ist aus dem gehäuften Auftreten massiger, geschwollener Spicula, z.B. *Thoracospongia* n. gen., die anscheinend nicht zusammen mit den dünnwandigen Protospongien vorkommen, ersichtlich. Das Oberdevon (Famenne) war die Zeit des Einsetzens der meisten Dictyospongiidae in deltaischen Environments des Staates New York. Aus dieser Zeit stammen auch die frühesten Vertreter der Hexactinosa, die meistens im unmittelbar vertikalen bzw. lateralen Anschluß an Riffentwicklungen vorkommen. Im Perm von Texas wurden von den Hexactinellidae verschiedene, ansonsten nur bei den Demospongiae bekannte Spiculatypen entwickelt. *Irpaspongia* MEHL & MOSTLER ist der einzige bekannte Fall der hexactinelliden Gerüstbildung durch Zygose, eine Strategie, die sonst nur innerhalb der Demospongiae verwirklicht ist. So finden sich innerhalb der Docodermatidae massenhaft „Oxen", „Toxen", „Triaene" und in einigen Taxa auch „Strongyle" (Abb. 13) (letzterer Spiculatyp ist innerhalb der Demospongiae eine Autapomorphie der Strongylophora REITNER, 1992). Diese Entwicklung demospongioider Spiculatypen innerhalb der Hexactinellida des Perms von Texas ist ein einzigartiges Beispiel einer Parallelevolution zwischen Hexactinellida und Demospongiae.

8. Systematischer Anhang

Gabelia fascicula RIGBY et al., 1991: der erste Fund eines Hexactinelliden der Nordamerikanischen Faunenprovinz in Europa.

Gabelia fascicula RIGBY et al., 1991
(Taf. VII, Fig. 2)

Beschreibung: Es handelt sich um ein vollständiges Exemplar, das als ganz flachgedrückter limonitischer Abdruck sowohl des Schwammkörpers als auch Stiels erhalten ist. Das Nadelskelett ist jedoch nur noch unvollständig in Form schlecht erhaltener Spicula-Abdrücke vorhanden. Der ovale, wahrscheinlich leicht deformierte Schwammkörper ist 27 mm breit, aber nur etwa 23 mm hoch. Sein zylindrischer, an der Basis abgerundeter Stiel ist 22 mm lang und 7 mm breit. Das Osculum ist nicht sichtbar und die Spicula-Abdrücke größtenteils zerstört. Nur im mittleren Bereich des Schwammkörpers sind diagonal angeordnete Stauractine zweier Größenordnungen erkennbar: Strahlenlänge der ersten Ordnung 1,5–2,0 mm, Strahlenlänge der zweiten Ordnung ca. 1,0 mm. Am Stiel sind nur andeutungsweise Abdrücke zu rektangulären Maschen in Längsreihen angeordneter Stauractine erkennbar.

Diskussion: Die Querschnitte der Originalexemplare von *Gabelia fascicula* zeigen, daß der Schwammkörper eine 4–6 mm dicke Wand besaß, die in einer äußeren und einer inneren Lage gegliedert ist (vgl. Rekonstruktion durch RIGBY et al., 1991: Fig. 4). Der äußere Bereich zeigt eine Protospongien-ähnliche Spikulation aus kleinen Spicula, überwiegend (bzw. ausschließlich?) Stauractinen in vertikalen und horizontalen Bündeln. Die innere Lage besteht aus etwas gröberen Stauractinen in diagonaler Anordnung. Am hier beschriebenen Exemplar sind anscheinend nur diese inneren Stauractine erhalten, deren Größenordnungen und diagonale Anordnung mit den Angaben der Originalbeschreibung gut übereinstimmen. Da nur die Spicula der Innenwand erkennbar sind und kein Osculum zu sehen ist, liegt die Vermutung nahe, daß das Schwammfossil mitten durch den Oscularraum aufgespalten sei, was sich allerdings erhaltungsbedingt nicht beweisen läßt.

Es handelt sich bei diesen Schwamm um das bisher erste aus Europa beschriebene Exemplar der Gattung *Gabelia*. Alle anderen Vorkommen der bisher drei Arten dieser Gattung, *G. pedunculus*, *G. giganta* und *G. fascicula* stammen aus dem Silur und Devon der Roberts Mountains Formation von Nevada, USA. Dieses Exemplar von *Gabelia fascicula* aus Nordwestdeutschland ist insofern von Interesse, als die vereinzelten Funde devonischer Hexactinelliden aus Europa bisher keine Beziehungen zu den reichen Vorkommen Nordamerikas erkennen ließen. Aus Europa kennen wir an devonischen Hexactinelliden in vollkörperlicher Erhaltung nur die Schwämme des Bundesbacher Schiefers (Siegen bis basales Ems) und die Hexactinosa des Heiligen-Kreuz-Gebirges (Frasnian). Der vorliegende Fund zeugt von einem gewissen Austausch zwischen den Hexactinelliden-Faunen des Devons von Nordwestdeutschland und Amerika, worauf es bisher keinerlei Hinweise gab. Diese scheinbar fehlende Beziehung der europäischen und nordamerikanischen Spongienfaunen stellt höchst wahrscheinlich eine Dokumentationslücke dar, die durch spätere Funde möglicherweise geschlossen werden kann.

Material: Das Exemplar (Stück und Gegenstück), leg. Dr. MALMSHEIMER (Bochum) wird am Paläontologischen Institut der Freien Universität Berlin aufbewahrt.

Stratigraphische Position: Grenzschichten Mittel-/Oberdevon.

Fundort: Enkenberg, Madfeld (Sauerland, Hessen, Deutschland).

Thoracospongia n. g.
(Taf. II, Figs. 1–7; Abb. 5)

Derivatio nominis: thorax (gr.) = der Panzer.
Typusart: *Thoracospongia follispiculata*
Locus typicus: Mittelkambrium des Georgina Basins, W-Queensland, Australien.

Diagnose: Hexactinellide mit panzerartigen äußeren Deckschichten aus stark geschwollenen, mit Längsrippen versehenen Hexactinen (Follipinulen).

Thoracospongia follispiculata n. g., n. sp.

Derivatio nominis: *follis* (lat.) = der Ballon.

Von dieser Art sind nur isolierte Follipinule bekannt. Eine hypothetische Rekonstruktion des Nadelskeletts dieser Art ist in Abb. 6 gezeigt. Die Spicula sind „aufgeblähte", in der Größenordnung zwischen 200 und 700 μm messende, durch unterschiedlich stark geschwollene und mit Längsrippen verzierte Distalstrahlen gekennzeichnete Pinuln, deren übrige Strahlen zu kleinen „Zapfen" reduziert sind. Der distale Strahl ist häufig wie ein Ball aufgebläht und kann mehr oder weniger stark auf das Achsenkreuz dieser Pinule übergreifen, sodaß dieses und auch die übrigen Strahlen „absorbiert" werden und kaum noch erkennbar sind. Solche „Kugeln" könnten auf den ersten Blick mit Sterrastern der Demospongiae verwechselbar sein.

Diskussion: Aufgrund der Beobachtung an rezenten Hexactinelliden, bei denen Pinule in der Regel in peripherer Position sind und die verdickten Nadeln eine äußere Cortex bilden, wird auch für *Thoracospongia* angenommen, daß es sich bei den Follipinulen um Dermalia handelt. In denselben Proben, welche solche Follipinule enthalten, finden sich auch um 200–400 μm große, stark geschwollene Triaxone, vor allem Stauractine, die wie prall gefüllte Kissen aussehen (Taf. I, Fig. 3-8; Taf. IV, Fig. 2; Taf. VII, Fig. 4). Möglicherweise gehören beide Typen „aufgeblähter" Spicula derselben Art, wie es in der Rekonstruktion (Abb. 5) angedeutet ist. Solange jedoch die Follipinule nur als isolierte Spicula bekannt und keine vollständigen Skelette gefunden sind, läßt sich diese Annahme nicht beweisen. Für die Diagnose entscheidend sind deshalb allein die Follipinule. Ähnliche Pinule, bei denen jedoch sämtliche Strahlen geschwollen sind, wurden von RIGBY (1975) aus der kambrischen Wilberns Formation, Texas, abgebildet. MOSTLER & MOSLEH-YAZDI (1976) haben Hexactine mit einigen stark geschwollenen Strahlen in oberkambrischen Sedimenten aus dem Elburzgebirge, Iran, gefunden. Keiner dieser Nadeltypen besitzt jedoch solche kugeligen mit Längsrippeln versehenen Distalstrahlen, wie sie für *Thoracospongia* charakteristisch sind. Ob diese spezialisierten Dermalia mit denen der später auftretenden „Brachiospongioidea" homolog sind, bleibt dahingestellt.

Material: Der Holotypus und ca. 30 weitere Exemplarewerden in der CPB, Bureau of Mineral Ressources, Canberra, Australien, aufbewahrt.

Hexatractiella n. g.
(Taf. IV, Fig. 4; Abb. 6, 7)

Derivatio nominis: *tractum* (lat.) = die Spinnwolle, bezieht sich auf die Längszüge von „verwobenen", gebündelten Spicula, bei denen es sich um modifizierte Hexactine handelt.

Typusart: *Diagoniella tubulare* RIGBY & HARRIS, 1979

Diagnose: Schwammkörper subzylindrisch mit gerundeter Basis ohne Wurzelschopf. Von der Basis bis zum Oskularrand erstrecken sich prominente divergierende Longitudinalbänder, die aus verlängerten Strahlen abgewandelter Hexactine bestehen. Dazwischen befinden sich mindestens vier Größenordnungen von Hexactinen in diagonaler Anordnung.

Beschreibung: Der zylindrisch bis konische, wenige, maximal bis 12 cm lange, manchmal verzweigte Schwammkörper ist dünnwandig mit einem tiefen Oskulum. Die Wand ist durchzogen von prominenten spiculären Zügen, die sich von der Basis bis zum oberen Rand verdicken und bis zu einem Abstand von ca. 5–6 cm divergieren. Diese Züge, deren Zahl von unten nach oben zunimmt (bis maximal 20), bestehen aus gebündelten Spicula, die zunächst wie Diactine anmuten. Bei genauerer Beobachtung zeigt sich jedoch, daß abgewandelte Triaxone mit jeweils einem oder zwei abgebogenen, stark verlängerten Paratangential-

strahlen diese Nadelzüge aufbauen. Zwischen den Zügen befinden sich diagonal angeordnete Triaxone in distinkten Größenordnungen, zahlenmäßig von zwei auf mindestens vier ansteigend. Die zwischen den Längszügen befindlichen, diagonal angeordneten Spicula erscheinen zunächst wie Stauractine, aber in großer Vergrößerung sind an deren Axialkreuzen häufig kleine Verdickungen und winzige Löcher von den Zentralkanälen ehemaliger Distal-/Proximalstrahlen zu beobachten, durch welche diese Spicula als Hexactine ausgewiesen sind.

Diskussion: *Hexatractiella* besitzt überwiegend, möglicherweise ausschließlich, hexactine Spicula. Diese sind zwar modifiziert mit atrophierten Distal- und Proximalstrahlen und z.T. extrem verlängerten Paratangentialstrahlen, aber der triaxiale Charakter, auch der zwischen den Zügen diagonal angeordneten Skleren ist eindeutig erkennbar (vgl. MEHL et al., 1993). Von *Diagoniella* RAUFF, 1894, sind ausschließlich stauractine Spicula bekannt. Die *Hexatractiella*-Spikulation läßt sich nicht aus dem Grundmuster der Gattung *Diagoniella*, oder dem eines Vertreters der Protospongiidae überhaupt, herleiten. Wohl aber kann sie aus einem Vertreter der Stammlinie Reticulosa, aus der durch die Modifikation hexactine Spiculazüge entstanden sind, hervorgegangen sein.

Nomenklatorische Notiz: Der Name „*Diagoniella ovata* RIGBY" in MEHL (1991: Fig. 1) ist ein *nomen nudum*. Der richtige Name dieses Schwammes aus dem Wheeler Shale ist *Diagoniella robisoni* RIGBY, 1978 (vgl. Taf. III, Fig. 1).

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Anschrift der Verfasserin:
Dr. Dorte Mehl, Institut für Paläontologie der Freien Universität Berlin, Malteserstr. 74-100, D-12249 Berlin.
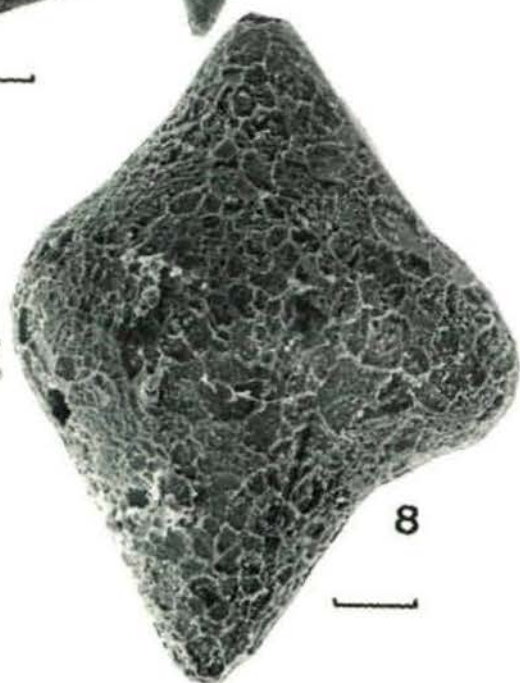
Tafel I

Spicula aus dem Mittelkambrium des Georgina Basins, Australien; REM, Maßstab 50 µm.

Fig. 1:   Tylodisk vom *Nabaviella*-Typ (?), CPC 33667.

Figs. 2–8: Extrem geschwollene triaxiale Spicula, größtenteils Stauractine. Dieser Nadeltyp kommt in der Regel mit Follipinulen gemeinsam vor; möglicherweise gehören sie zum Dermalskelett von *Thoracospongia follispiculata* (vgl. Text-Abb. 5).

Figs. 2–5, 8: CPC 33668, Fig. 6: CPC 33669, Fig. 7: CPC 33670.

CPC = Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology & Geophysics, Canberra, Australia.

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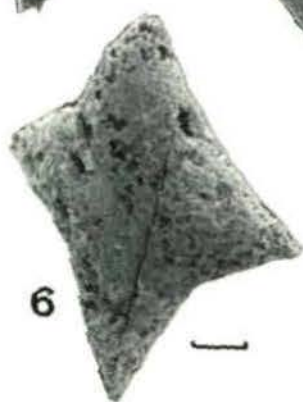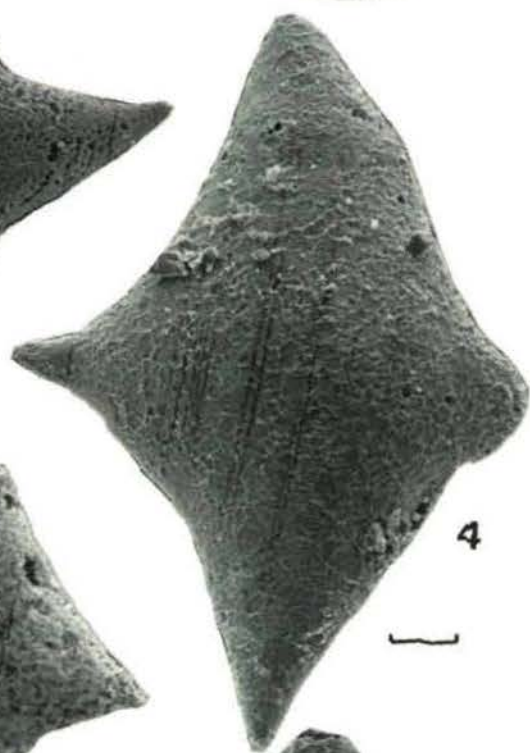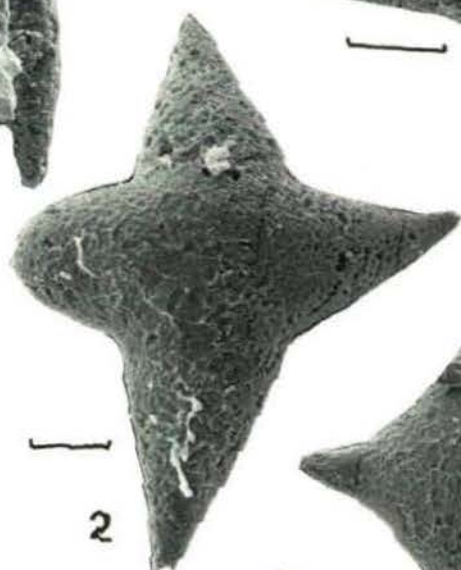
Tafel II

Spicula aus dem Mittelkambrium des Georgina Basins, Australien; REM, Maßstab überall 50 µm.

Figs. 1–7:   *Thoracospongia follispiculata* n. g., n. sp., vgl. auch Text-Abb. 4.
     Fig. 1: Holotypus, CPC 33671.
Figs. 2–7:   Paratypoide.
     Figs. 2, 4, 5: CPC 33672, Fig. 3: CPC 33673, Fig. 6, 7: CPC 33674.
Figs. 8–9:   Demospongioide Spicula der Gattung *Carphites* (Docodermatidae, Hexactinellida) aus dem Perm von
     West- Texas (Originale zu FINKS, 1960). REM, Maßstäbe 50 µm.:
Fig. 8:   Strongyl aus dem Wurzelschopf von *Carphites diabolensis*; USNM 78894.
Fig. 9:   Oxe von *Carphites plectus*; USNM 127662a.
     USNM = Unites States National Museum, Smithsonian Institution, Washington D.C., USA.
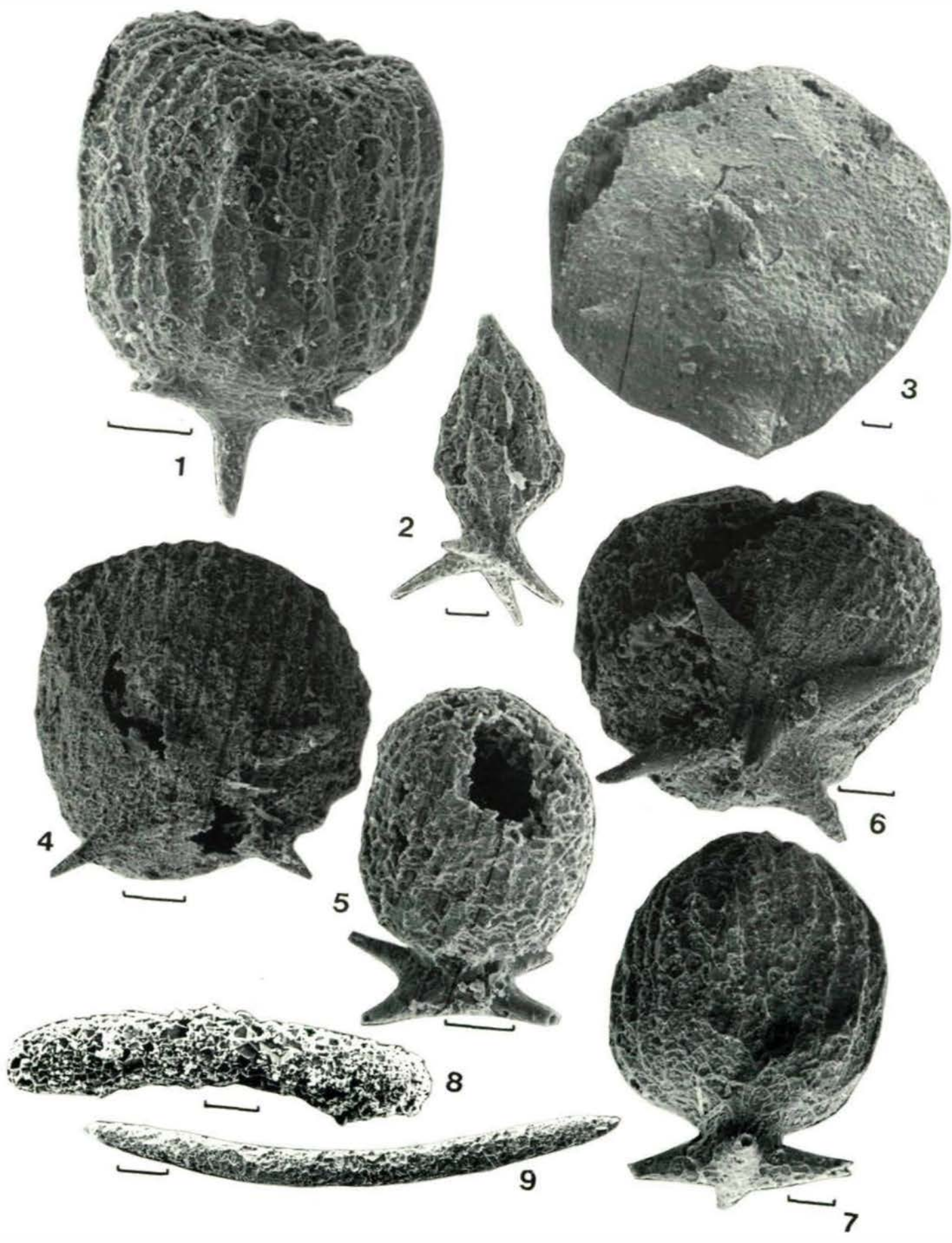
Tafel III

Fig. 1:   *Diagoniella robisoni* RIGBY, 1978, aus dem mittelkambrischen Wheeler Shale, Utah. Maßstab 5 mm.

Fig. 2:   *Protospongia tetranema* DAWSON, 1888, aus der DAWSON-Collection von Little Métis, Ordovizium. Das Ty-
pusmaterial wurde zur Verschönerung vom Autor z.T. bemalt und „ergänzt", und die weißen Kreuze und
„Diactine", die in Publikationen mit abgebildet wurden, sind außer durch die weiße Farbe in den Typusexem-
plaren nicht immer erkennenbar. Redpath Mus. 2.316. Maßstab 1 cm.

Fig. 3:   *Protospongia hicksi* HINDE, Original zu RIGBY, 1966, aus dem kambrischen Marjum Limestone.
USNM 145295. Maßstab 7 mm.

Figs. 4–5: Kometiaster aus dem Georgina Basin. CPC 33675. REM; Maßstab 100 μm.
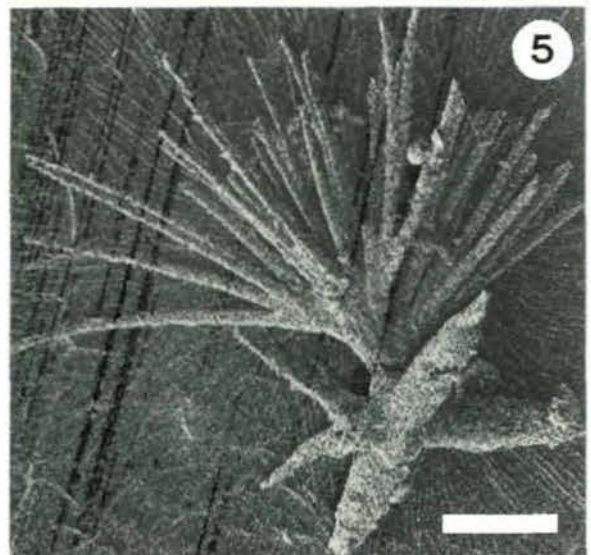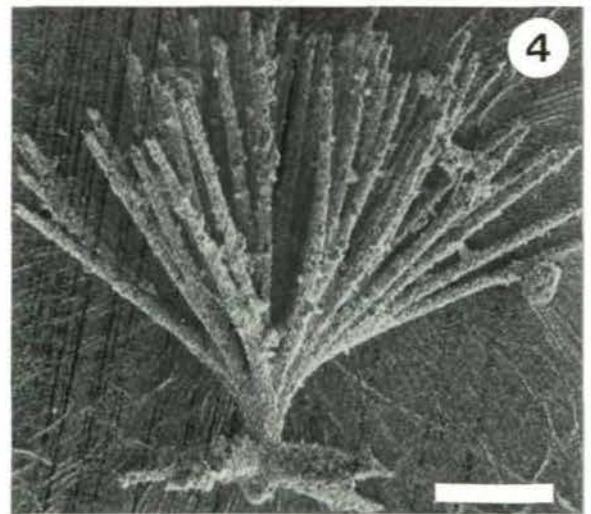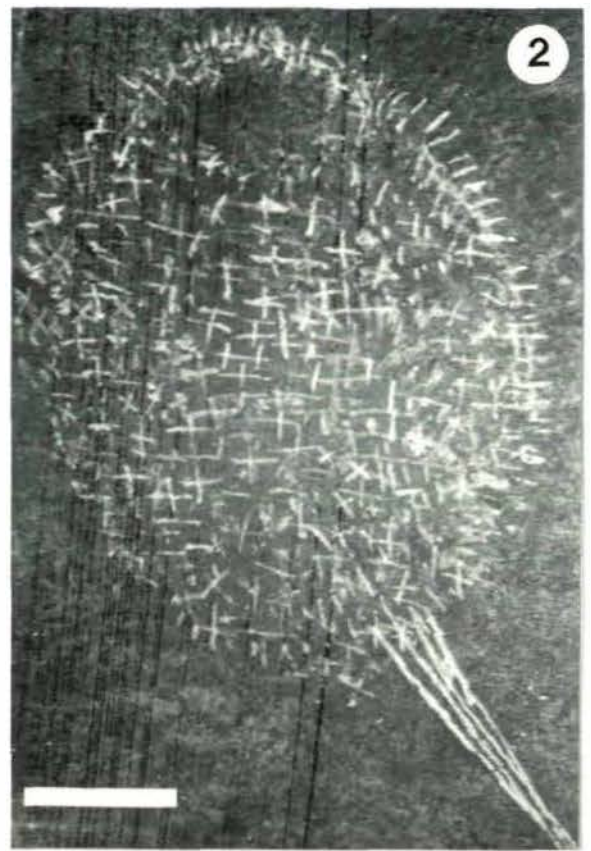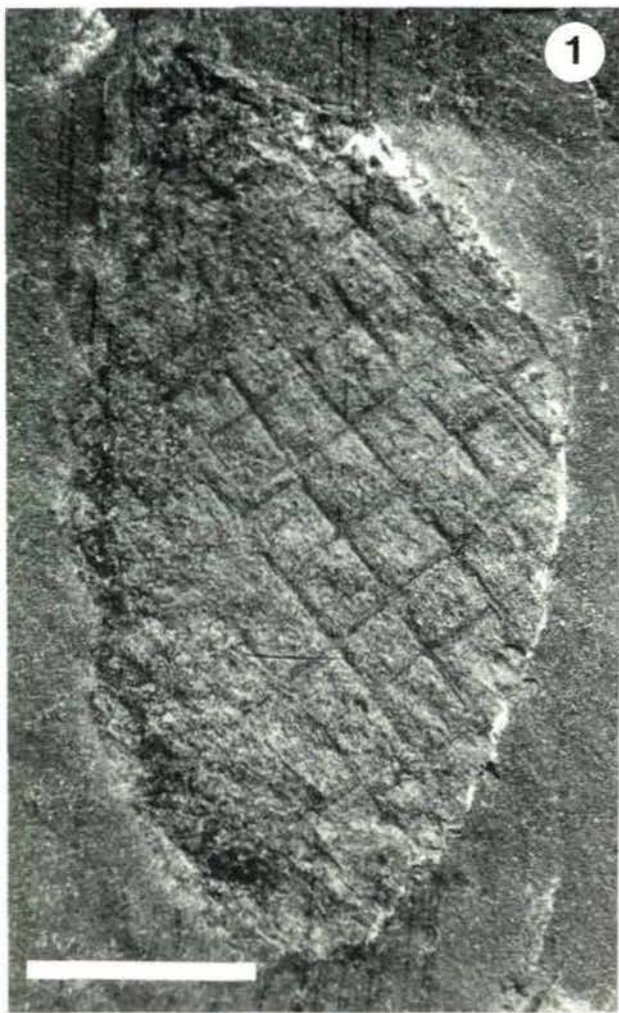
Tafel IV

Fig. 1: *Mattaspongia apaches* RIGBY, 1970, aus dem späten Devon von Alberta; Paratypoid (Foto RIGBY, mit freundlicher Erlaubnis). Maßstab 10 mm.

Fig. 2: Stark geschwollener Hexactin aus dem mittelkambrischen Georgina Basin, CPC 33676,. Maßstab 1 mm.

Figs. 3, 5: Lyssakine Spikulation von *Ammonella quadrata* WALTHER, 1904, aus dem Solnhofener Plattenkalk (Tithon, Südwestdeutschland) mit Stauractinen in regelmäßiger quadratischer Anordnung. Dieser hexactinellide Schwamm aus dem späten Jura zeigt eine starke Affinität zu den Protospongiidae. Ob es sich hierbei um eine Homoplasie oder aber um eine überlebende protospongiide Art aus dem Altpaläozoikum handelt, läßt sich derzeit nicht entscheiden. Weitere Erläuterungen im Text.

Fig. 4: *Hexatractiella nevadensis* (RIGBY & STUART, 1988) Silur-Devon-Grenzschichten in Nevada. Abgewandelte Hexactine verschiedener Größen bilden die Spicula-Längszüge scheinbarer „Diactine". Maßstab 1 mm.
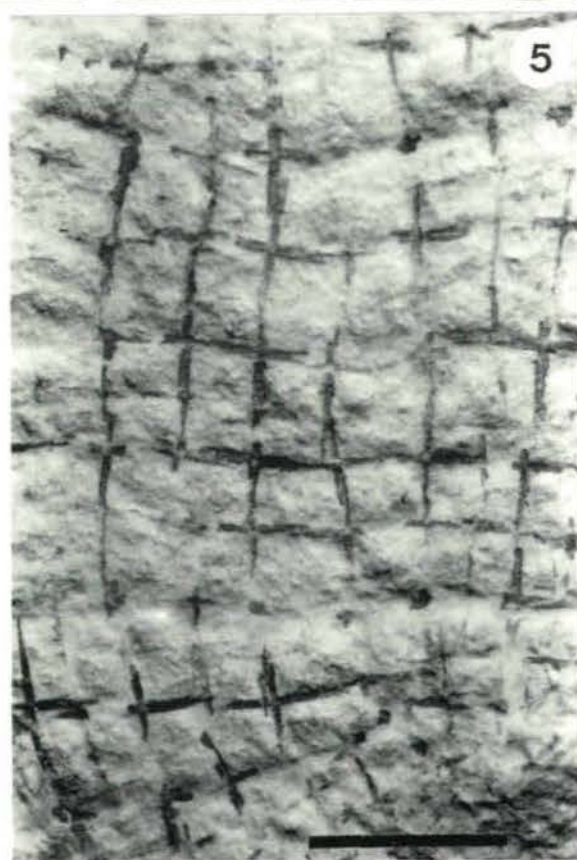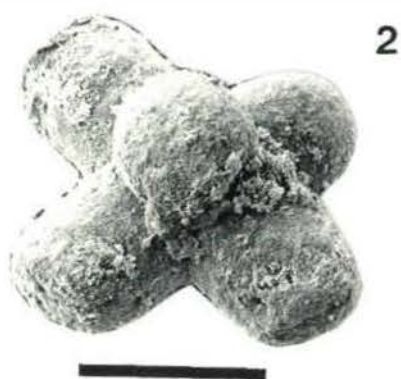
Tafel V

Fig. 1: Hexactinosa sp. aus dem Oberdevon (Frasné) des Heiligen-Kreuz-Gebirges, Polen. REM, Maßstab 250 μm.

Fig. 2: *Hydnoceras* sp. (Dictyospongiidae) aus Mansfield („Chemung"), USNM 33562. Maßstab 2 cm.

Fig. 3: Dünnschliff des Diktyonalskeletts eines Hexactinosa sp. aus dem Oberdevon (Frasné) von Elbingerode, Harz. Maßstab 200 μm.

Fig. 4: Hemidisk von *Microhemidiscia ortmanni* KLING & REIF, 1969, Holotypus, Tüb. 1340/5. Maßstab 100 μm.

Fig. 5: Dichte Züge von Oxen und andere demospongioide Spicula aus dem subdermalen Bereich von *Carphites plectus* FINKS, 1960, USNM 127662a. REM, Maßstab 500 μm.

Fig. 6: Desmoides Sklerenskelett von *Pileolites baccatus* FINKS, 1960, USNM 78863. Maßstab 50 μm.

Distance = 210µ
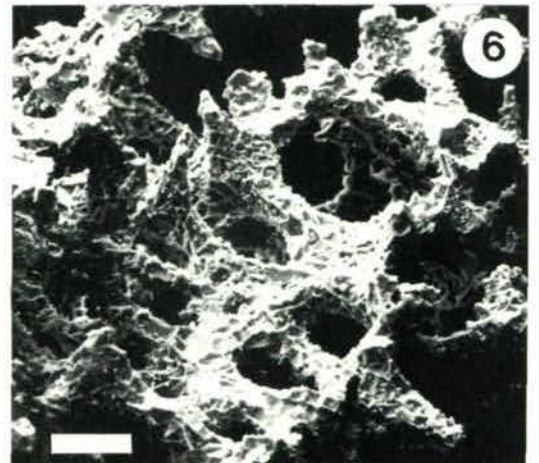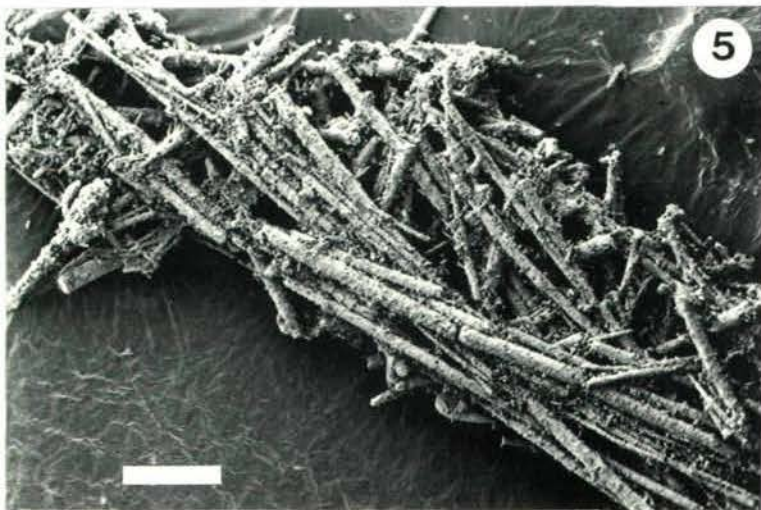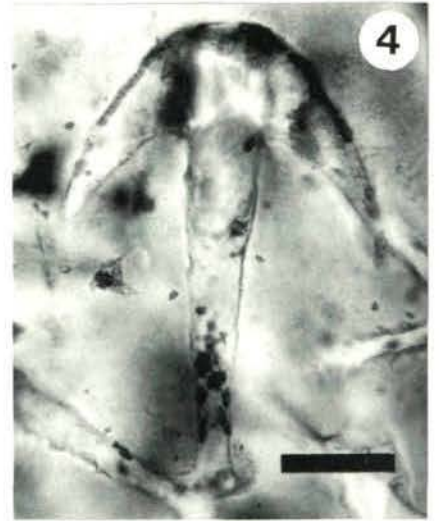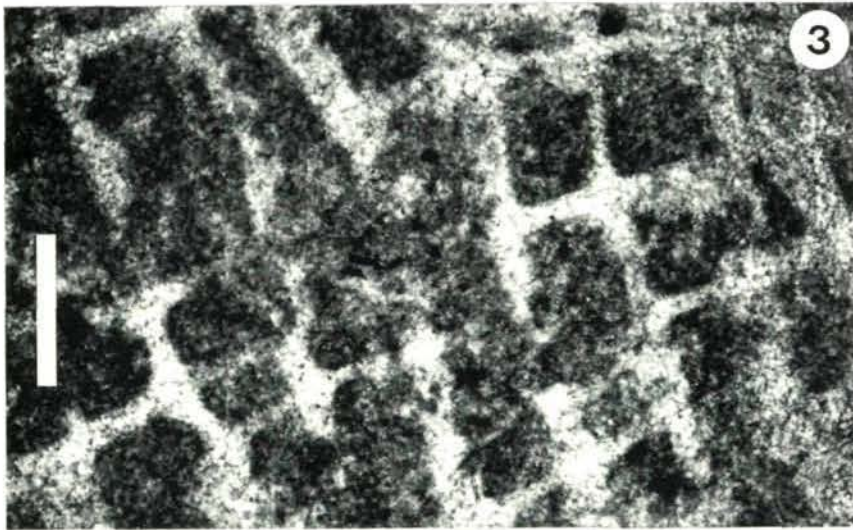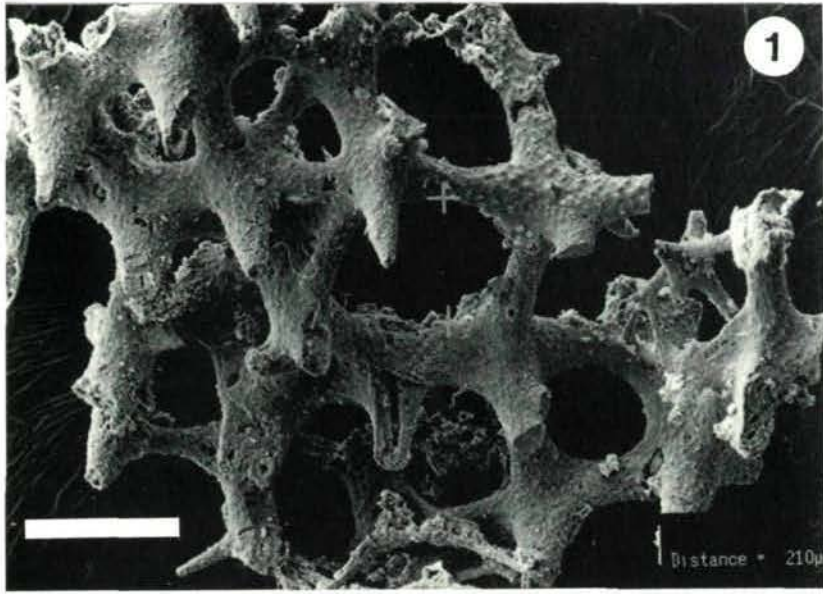
Tafel VI

Brachiospongia digitata (OWEN, 1858) Ordovizium, Kentucky Shale; (Foto RIGBY m. freundl. Erlaubnis). Maßstab 3 cm.

Fig. 2:   Anhäufung kleiner Exemplare von *Teganiella ovata* RIGBY & MEHL aus dem Mitteldevon von Simpson Park, Nevada. Die sowohl größenmäßige als auch artliche Sortierung gibt sedimentologische und palökologische Hinweise, vgl. Text-Abb. 12. Maßstab 5 mm.

Fig. 3:   Vergleichbare Anhäufung kleiner Spongien der Art *Choia ridley* WALCOTT, 1920 (Demospongiae) auf einer Schichtfläche aus dem Burgess Shale läßt ähnliche Mechanismen vermuten. Maßstab 10 mm.

Figs. 4–5: *Pileolites baccatus* FINKS, 1960, USNM 78863, Maßstab 100 µm.

Fig. 4:   Desmoides Gerüst (Tetraclone ?). REM.

Fig. 5:   Äußere Deckschicht mit kugeligen Schwellungen.
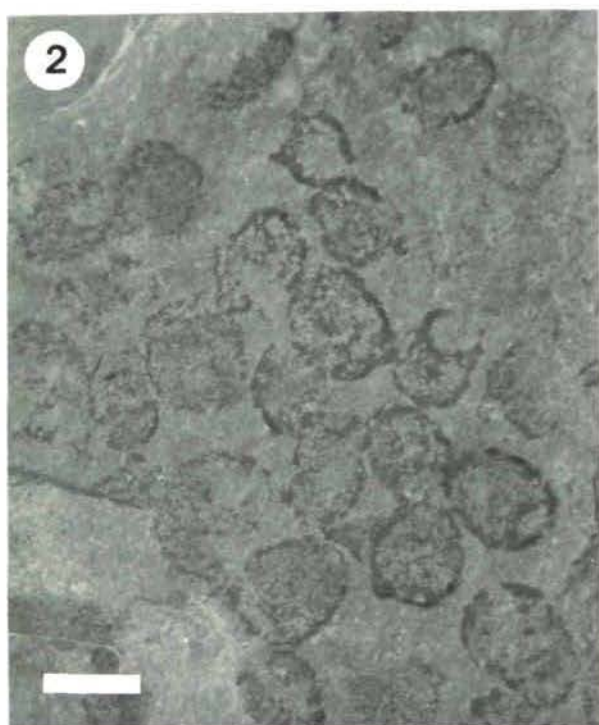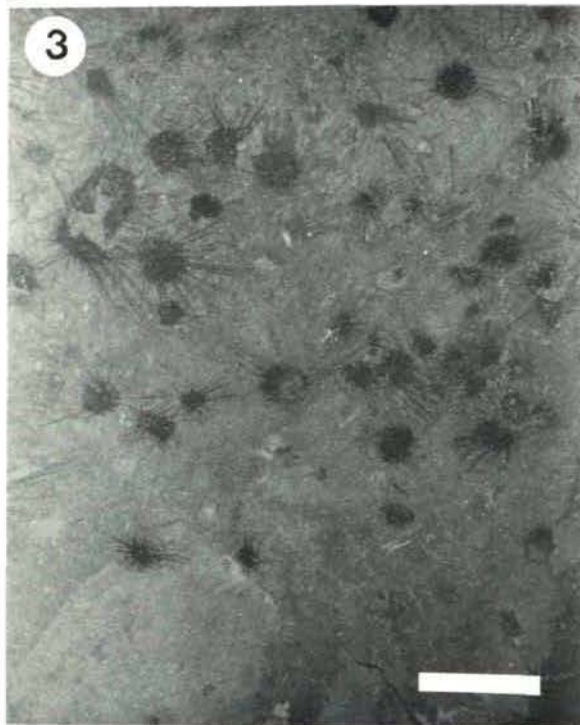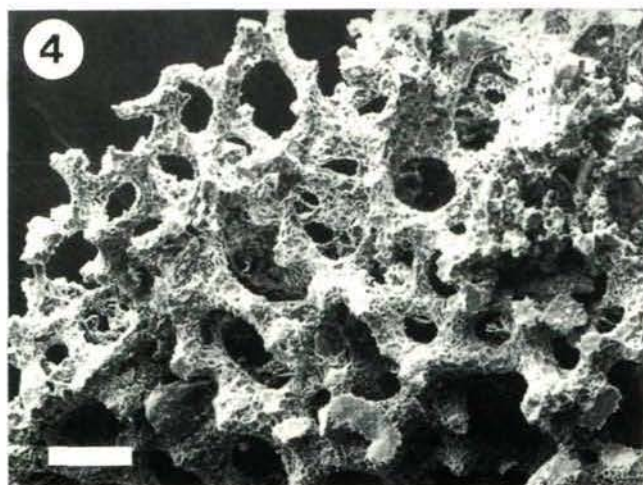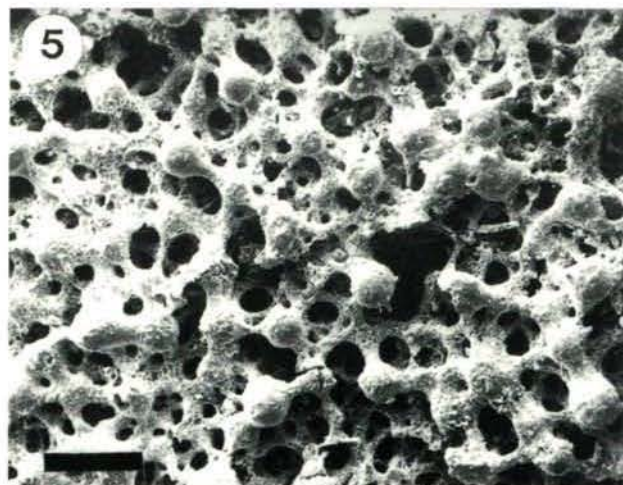
Tafel VII

Fig. 1: *Sanshapentella dapingi* MEHL & ERDTMANN, 1994, Holotypus, aus dem Tommotium von Sansha (N-Hunan, China). Maßstab 5 mm.

Fig. 2: *Gabelia fascicula* RIGBY et al., 1991. Exemplar aus Grenzschichten des Mittel-/Oberdevons vom Madfeld im Sauerland (Nordwestdeutschland); Beschreibung siehe Anhang. Maßstab 5 mm.

Fig. 3: *Cyathophycus rhenana* (SCHLÜTER, 1892) aus dem Bundenbacher Schiefer (Unterdevon, Westdeutschland), leg. BRASSEL (SNG 218). Spicula-Anordnung der Spongienwand (vgl. Text-Abb. 10). Maßstab 2 mm.

Fig. 4: Stark geblähtes diactines Spiculum aus dem Mittelkambrium des Georgina Basins (CPC 33677). Maßstab 100 μm.

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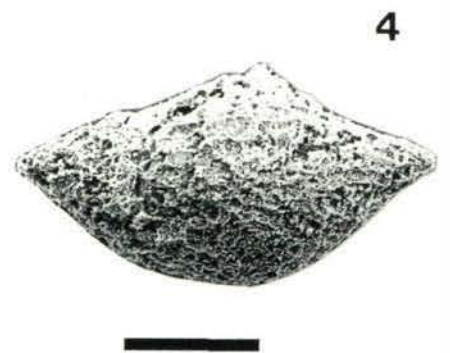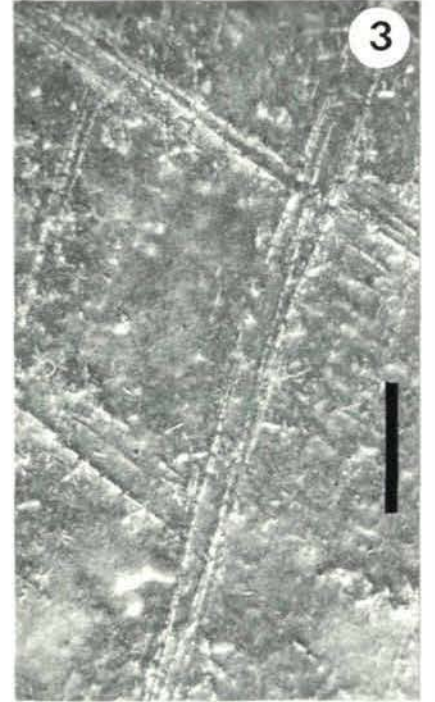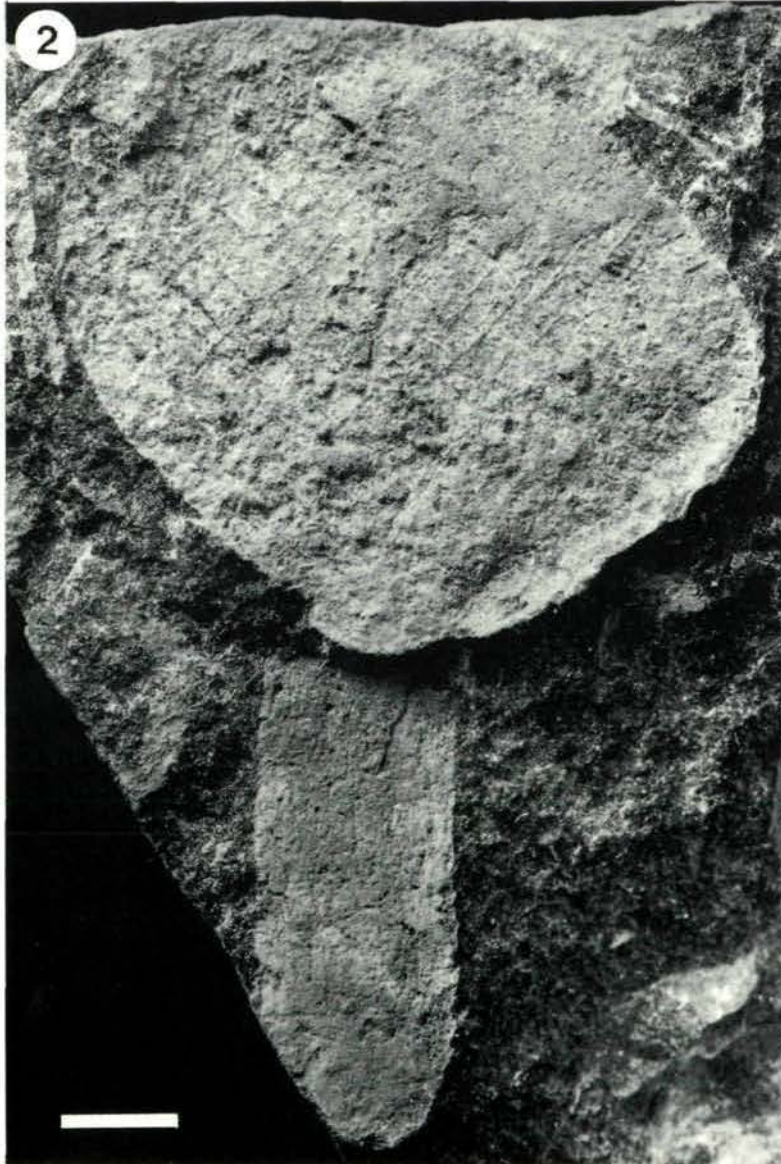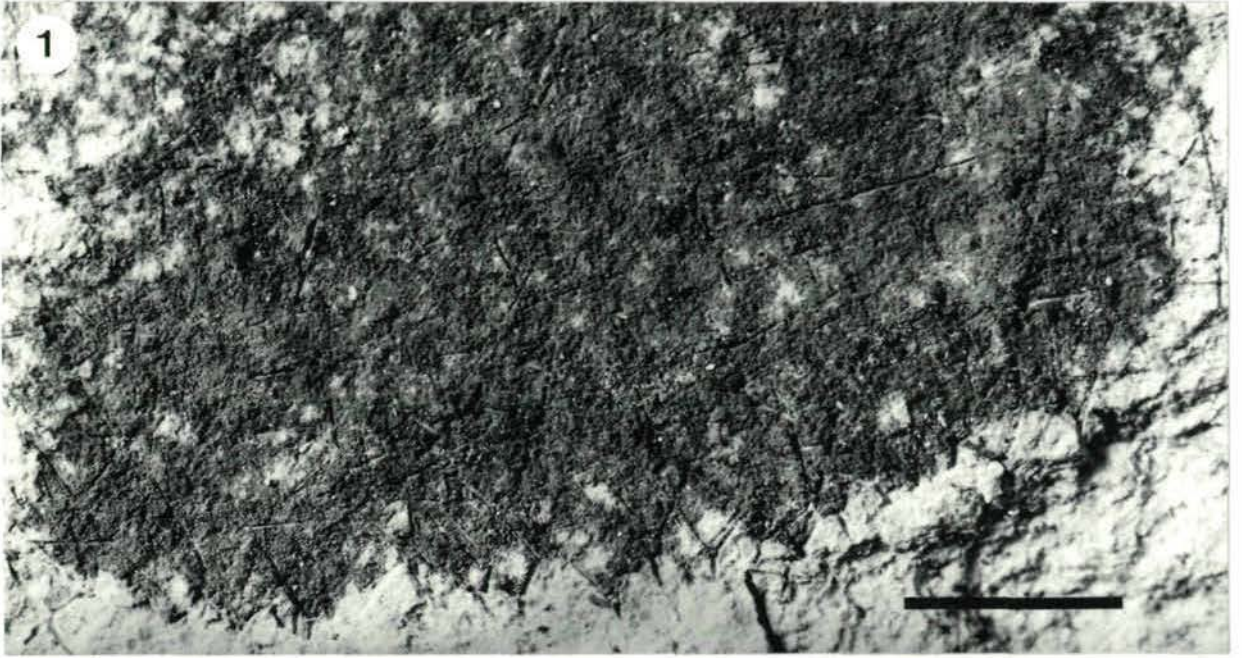
NEW MICROBIOSTRATIGRAPHICAL DATA FROM SEVERAL LOWER CRETACEOUS PELAGIC SEQUENCES OF THE NORTHERN CALCAREOUS ALPS, AUSTRIA (PRELIMINARY RESULTS)

Daniela Reháková, Jozef Michalík & Ladislava Ožvoldová

With 7 figures and 5 plates

Abstract:
The article gives a survey of results of microfacies and microbiostratigraphic investigation of Lower Cretaceous pelagic limestone sequences of six selected sections in Eastern Alps. The study contributes to the more widely oriented correlation IGCP Project No. 362, as well as to ALCAPA Project. Attention was focused on distribution of the calpionellid microfauna in Texing, Reidl, Hohenberg, Großer Flösselberg, Anzenbach and Gartenau sections as well as on radiolarian associations in the Hohenberg and Gartenau sections. The correlation of lithostratigraphic units coming from different paleotectonic environments was enabled by combined utilization of various biostratigraphic markers (calpionellids, radiolarians, but also ammonites, etc.) and of several parallelly developed biostratigraphic scales. Preliminary results of this complex study indicate possible calibration of variations in index microfossil distribution in individual sedimentary basins often affected by local factors.

Zusammenfassung:
In dieser Studie werden die Ergebnisse der mikrofaziellen und mikrobiostratigraphischen Untersuchungen pelagischer Karbonatgesteinsfolgen anhand von sechs Profilen der Nördlichen Kalkalpen dargestellt. Die Untersuchungen stellen sowohl einen Beitrag zum IGCP-Projekt Nr. 362, als auch zum ALCAPA-Projekt dar. Besonderes Augenmerk wurde auf die Verbreitung der Calpionellen in den Profilen Texing, Reidl, Hohenberg, Großer Flösselberg, Anzenbach und Gartenau gelegt. Aber auch die Erfassung der Radiolarienfauna in den Profilen Hohenberg und Gartenau war ein besonderes Anliegen. Durch den kontinuierlichen Einsatz verschiedener biostratigraphischer Marker (Calpionellen, Radiolarien, aber auch Ammoniten etc.) war es möglich, die lithostratigraphischen Einheiten aus den verschiedensten paläotektonischen Ablagerungsräumen zu korrelieren. Die vorläufigen Ergebnisse der Studie zeigen auf, daß die Eichung von Index-Mikrofossilien in den jeweiligen Becken oft stark von lokalen Faktoren beeinträchtigt wird.

Introduction

In the frame of the ALCAPA partial project "Cretaceous and Paleogene paleogeography and geodynamics of the Alpine-Carpathian-Pannonian Region", led by Prof. Dr. F. Faupl from the Geological Department of the University of Vienna, field works were organized with aim to establish a basis for detailed lithostratigraphic correlation and interpretation of sedimentary regime in Lower Cretaceous Alpine-Carpathian basins. Samples from six selected sections (Figs. 1, 2) representing Lower Cretaceous sequences of several Penninic, Bajuvaric and Tirolic units of the Eastern Alps were collected during field season in summer 1992.

The investigation of Lower Cretaceous microplankton is closely connected with orientation of the IGCP Project 362 (Tethyan and Boreal Cretaceous Correlation). In the last few years, biostratigraphical scales based on different organisms were correlated (ONDREJÍČKOVÁ et al., 1993; VAŠÍČEK et al., 1992, 1994 a, 1994 b). Special attention was focused on local variations of microplankton associations in various Tethyan regions (REHÁKOVÁ & MICHALÍK, 1992, 1993, 1994).

The study of Upper Jurassic and Lower Cretaceous sequences stressed the need of more precise lithologic and biostratigraphic calibration, enabling more reliable correlation of neighbouring sedimentary basins. In this aspect, several widely used lithostratigraphic terms (e. g. "Aptychen-
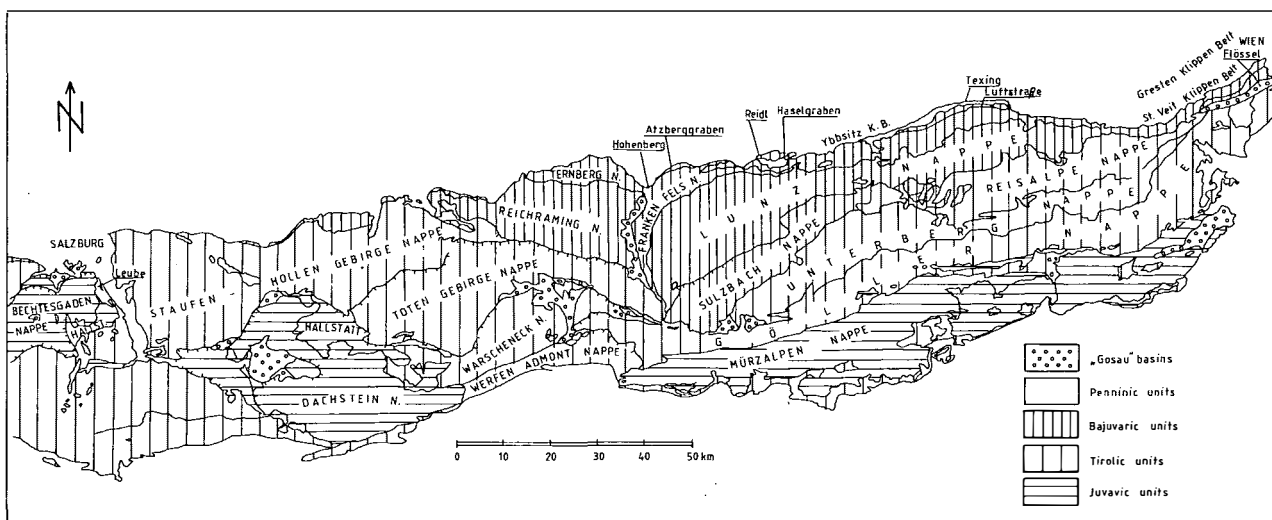
Fig. 1: Microbiostratigraphically investigated sections in Upper Jurassic and Lower Cretaceous sequences in the Austrian Eastern Alps.

kalk") do not answer to modern lithostratigraphic classification.

Calpionellid microbiostratigraphy was developed by authors working in Jurassic Cretaceous sequences of Western Alps footmountains (REMANE, 1964; REMANE, in BOLLI et al., 1985). A few years later, the calpionellid zonation was applied and refined in the Carpathians, too (NOWAK, 1970; POP, 1974; BORZA, 1984; BORZA & MICHALÍK, 1986). Simultaneously, several pecularities in calpionellid distribution became more pronounced. Unfortunately, Upper Jurassic – Lower Cretaceous calpionellid associations in the East Alpine pelagic limestone sequences which could fill the gap between the two areas mentioned were inadequately investigated only (KRISTAN-TOLLMANN, 1962; FLÜGEL & FENNINGER, 1966; GARRISON, 1967; HOLZER, 1968; FENNINGER & HOLZER, 1970; WIDDER, 1988).

The Jurassic and Lower Cretaceous radiolarian biostratigraphy was used for correlation of deep-sea deposits (PESSAGNO, 1977). It was adapted by BAUMGARTNER et al. (1980, 1984, 1987) and SCHAAF (1984, 1985) for the Mediterranean Tethys. Interest of stratigraphers is concentrated on its correlation with the calpionellid and ammonite zonations.

1.1. Setting

1. The Texing section in the Penninic Gresten Klippen Belt is exposed by a road cut to the Plankenstein Castle southwest of St. Pölten (Fig. 1). Upper Jurassic fluxoturbidites (Scheibbsbach and Konradsheim Fms) and pelagic limestones (Arzbergkalk) crop out above Middle Jurassic cherty sequence (Lampelsberg Fm). 22 samples were taken from the Lower Cretaceous rhythmical limestone- and marly complex belonging to the Blassenstein Fm. It is overlain by Middle Cretaceous variegated marls (Buntmergel Gp, Fig. 2).

2. The Penninic Ybbsitz Zone is represented by the Reidl section, exposed by a small quarry WSW of Ybbsitz and southward from Amstetten (OŽVOLDOVÁ & FAUPL, 1993). Middle Jurassic silicites (Rotenberg Fm) are followed by pelagic limestones (Fasselgraben Fm, nine samples) with breccia and turbidite beds. Valanginian to Coniacian turbidite sequence of marly siltstones to sandstones with breccia and claystone intercalations (Glosbach, Haselgraben and Ybbsitz Formations) forms its overlying.

Age	PENNINIC		BAJUVARIC			TIROLIC
	Gresten Zone	Ybbsitz Zone	Frankenfels	Lunz Nappe	Reichraming	Staufen N.
CENOMANIAN	Buntmergel Group	Ybbsitz Fm Haselgraben Formation	Losenstein Beds	Itruvia B. ~~~~~~~~		?
ALBIAN			Tannheim Beds	?	?	
APTIAN	Blassenstein Formation		3	?		Grabenwald ----- Fm
BARREMIAN		Glosbach Formation		R o s s f e l d		
HAUTERIVIAN	1			F o r m a t i o n		
VALANGINIAN		2	S c h r a m m-	4	5	-Anzenbach-
BERRIASIAN		Fassel- graben Formation	b a c h	F o r m a t i o n		6
TITHONIAN						
KIMMERIDGIAN	Konradsheim Arz-___F	—?—?—?—	S t e i n m ü h l L i m e s t o n e	O b e r a l m F o r m a t i o n		
OXFORDIAN	‾berg Lst Scheibbsbach	Rotenberg Beds				

Sections:

1 - Texing,   2 - Reidl,   3 - Hohenberg,   4 - G. Flösselberg,   5 - Anzenbach,   6 - Gartenau

Fig. 2: Lithostratigraphy of Upper Jurassic and Lower Cretaceous formations in selected Austroalpine units.

3. The Hohenberg section in a forest road cut above Anzenbach south from Steyr represents Frankenfels Nappe development (Rettenbach Mulde) of the Bajuvaric. Upper Jurassic to Berriasian nodular Steinmühl Limestone is covered by Schrambach Formation built of thin-bedded spotted marly limestones intercalated by marls. The latter pass into blackish marlstones with marly limestone intercalations belonging to the Tannheim Fm (Fig. 2). Albian to Cenomanian Losenstein Fm is formed by a shaly complex with rhythmic sandstone intercalations.

4. Lunz Nappe of Bajuvaric is represented by a section in the Perlmooser Zementwerke Quarry on the Großer Flösselberg near Kaltenleutgeben (Wienerwald) at the southwestern periphery of Vienna. There is a complex of nodular limestones (Steinmühl Fm) covered by cement marls and well-bedded grey spotted limestones with allodapic intercalations (Schrambach Fm). Turbidites of the Roßfeld Formation follow with erosional unconformity above it.

5. Tirolic Lower Cretaceous pelagic sequence has been studied in Leube brothers cement quarry

in Gartenau near St.Leonhard southward from Salzburg. Upper Jurassic Oberalm Fm comprising slumped bodies of Permian, Triassic and Lower Jurassic rocks (PLÖCHINGER, 1974; MATURA & SUMMESBERGER, 1980) are covered by a thick complex of well-bedded spotted marly limestones of Schrambach Fm, capped by reddish marly Anzenbach Limestone. The sequence it terminated by sandy marly and conglomeratic (olisthostrome- rich) Roßfeld Fm.

2. Lithostratigraphy and microfacies

2.1.Penninic units

These sequences represent the record of a synrift sedimentation in the Penninic Ocean, which has been spreading during Jurassic and Lower Cretaceous. The rests of their sediments were mostly subducted during Alpine orogenesis, only being preserved in two zones of tectonic slices. The Gresten Klippen Belt is characterized by fluviatile to shallow-marine Lower and Middle Jurassic Gresten Beds, followed by pelagic cherts (Lampelsberg Fm) and limestones (Blassenstein Fm), and then by the Buntmergelserie of Cretaceous to Eocene age (Fig. 2). On the other hand, the Ybbsitz Klippen Belt contains an ophiolite sequence (HOMAYOUN & FAUPL, 1992), represented by ultrabasics and basic rocks, Mn cherts, radiolarites (Rotenberg Fm) and pelagic limestones (Fasselgraben & Glosbach Fms). The sedimentation continued by Cretaceous flysch (Haselgraben Fm).

2.1.1. Gresten Zone (Texing section)

Bedded dark-gray silicified mudstone contains sporadic pyritized radiolarians, sponge spicules and *Colomisphaera tenuis* (NAGY). Overlying variegated marly pelbiosparites contain *Textularia* sp., *Cadosina semiradiata semiradiata* WANNER, *Cad. fusca fusca* WANNER, *Cad. parvula* (NAGY), *Colomisphaera radiata* (VOGLER),

Schizosphaera minutissima (COLOM), *Carpistomiosphaera tithonica* NOWAK, bivalve shell fragments, crinoids, aptychi, pellets with silicified nuclei, rhombs of authigene feldspars, silt quartz and glauconite grains. The association of microfossils (Fig. 3) is typical of Early Tithonian Tithonica Zone.

Overlying indistinctly nodular limestones contain microfossils of the Early Tithonian Malmica Zone: *Parastomiosphaera malmica* BORZA, *Cadosina fusca fusca, Colomisphaera carpathica* (BORZA), *Globochaete alpina* LOMBARD, *Saccocoma* sp., foraminifer fragments, crinoids and aptychi. Slightly silicified sediment contains silty admixture of quartz, mica and glauconite.

A few fluxoturbidite intercalations (up to 25 cm thick) are built of gray fine-grained organodetrital limestone with biopelmicrosparite texture. It contains *Carpistomiosphaera tithonica, Cadosina semiradiata semiradiata, Cadosina fusca fusca, Pieninia oblonga, Textularia* sp., *Quinqueloculina* sp., *Parastomiosphaera malmica,* foraminifer fragments, crinoids, aptychi, bivalves and ostracods. The presence of fluxoturbidite intercalations in the described part invokes a comparison with the upper member of the Konradsheim Formation.

Pale micrites of the Majolica type belong to calpionellid, calpionellid-radiolarian and radiolarian wackestone to mudstone. Bed thickness decreases upwards. The lower part of the complex contains microfossils of the Late Tithonian Crassicollaria Zone: *Crassicollaria intermedia* (D. DELGA), *Cr. colomi* DOBEN, *Cr. parvula* REMANE, *Calpionella alpina* LORENZ, *Tintinnopsella carpathica* (MURGEANU et FILIPESCU), *Schizosphaerella minutissima, Cadosina fusca fusca, Globochaete alpina,* calcified radiolarians, foraminifer fragments, crinoids and bivalves. While the lithology of Berriasian limestones remains unchanged, microfossil association (Fig. 3) is dominated by sphaerical form of *Calpionella alpina,* later accompanied by *Remaniella ferasini, R. cadischiana* (COLOM) and *Calpionella elliptica* CADISCH.

Thin-bedded pale gray-spotted limestone with rhythmic marly intercalations (biomicrite of mudstone/wackestone type) is the most typical member of the Blassenstein Formation. It contains mi-

Fig. 3: Microbiostratigraphic evaluation of the Texing section, Gresten Klippen Belt, Penninic, Eastern Alps.
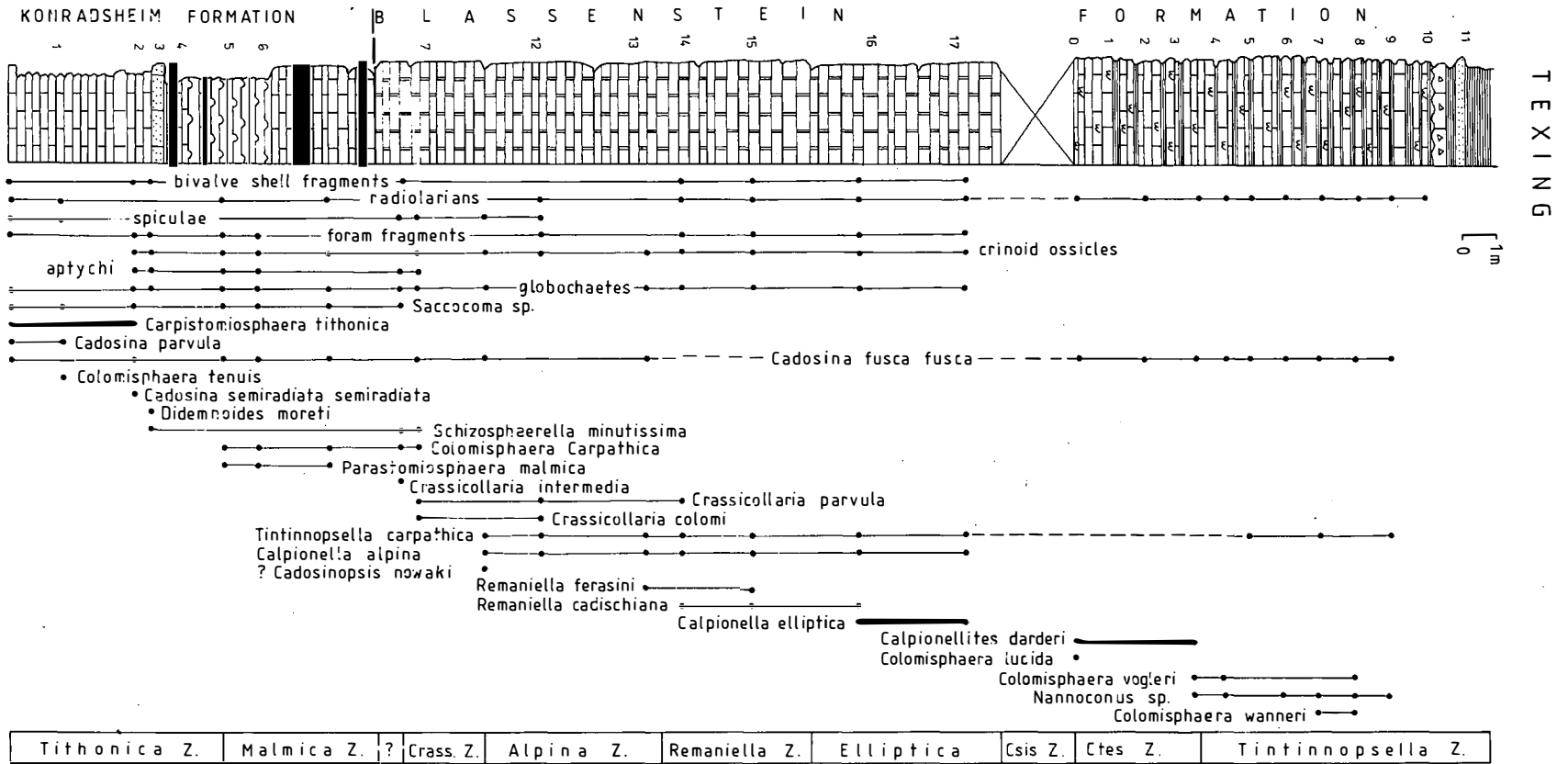
crofossils ·of Late Berriasian to Early Valangin-ian Calpionellites Zone: *Calpionellites darderi* (COLOM), *Cadosina fusca fusca, Colomisphaera lucida* BORZA, *Col. vogleri* (BORZA), *Col. wanneri* BORZA, accompanied by abundant nannoconids. Substantially reduced composition of microfossil association in the upper part of the sequence indicates Valanginian Tintinnopsella Zone.

2.1.2. Ybbsitz Zone (Reidl section)

Radiolarian associations of the Rotenberg Formation were evaluated in detail by OŽVOL-DOVÁ & FAUPL (1993). They indicate middle Callovian to late Oxfordian ·age of the chert sequence.

The lower member of the Fasselgraben Formation consists of indistinctly nodular limestone. The samples taken from its base contain microfossils (Fig. 4) of late Tithonian Crassicollaria Zone: *Crassicollaria parvula, Cr. massutiniana,* both elongated and sphaerical forms of *Calpionella alpina, Tintinnopsella carpathica, Globochaete alpina, Schizosphaerella minutissima.* The problem concerning indentification of the Kimmeridgian interval in this sequence (cf. DECKER, 1990) remains unsolved.

Higher-up lying well-bedded pale "Majolica" type micrite limestone comprises allodapic intercalations (distal turbidites, cf. HOMAYOUN & FAUPL, 1992). Microfossil content (Fig. 4: *Calpionella alpina, C. minuta, Remaniella ferasini* (CA-TALANO), *R. filipescui* POP, *Tintinnopsella· carpathica, Crassicollaria parvula, Cadosina fusca fusca, Colomisphaera carpathica, Schizosphaerella minutissima, Didemnum carpaticum, Globochaete alpina, Nannoconus sp.,* accompanied by aptychi fragments, foraminifers, ostracods, bivalves, crinoids and belemnites) indicates early/middle Berriasian age.

The clasts in breccia beds were derived from Kimmeridgian Saccocoma-Globochaete packstone with *Colomisphaera pieniniensis, Cadosina parvula*; lower Tithonian Saccocoma wackestone with *Parastomiosphaera malmica, Cadosina fusca fusca, Globochaete alpina,* radiolarians, ap-

tychi and juvenile ammonites: Berriasian Calpionella wackestone with *Calpionella alpina, Tintinnopsella carpathica, Colomisphaera· carpathica*; pelbiosparites with foraminifer fragments; sucrosic dolomitic and siliceous limestones; cherts and shales. Matrix of the breccias contains dispersed quartz (up to 2 mm in diameter) and glauconite grains.

2.2. Bajuvaric units

Upper Jurassic and lower Cretaceous sediments of these units have been deposited in a system of subsiding basins and elevations in the western part of the Alpine-Carpathian microcontinent (Fatric and Hronic units of the Central Western Carpathians form their eastward continuation, cf. MICHALÍK, 1994). Microfacies of pelagic elevations of this age (as well as their calpionellid microfauna) in the Frankenfels Nappe (Pechgraben area) have been described by KRISTAN-TOLLMANN (1962) and HOLZER (1968).

2.2.1.Frankenfels Nappe (Hohenberg section)

Red nodular biomicrite limestone – called the Steinmühl Limestone – forms a considerable part of the Kimmeridgian/Lower Valanginian sequence in the Rettenbach Mulde of the Frankenfels Nappe (FLÜGEL, 1967). Despite several problems caused by expressive condensation of this sequence, the following microfacies units could be distinguished:

a. The lowermost, Kimmeridgian member is built of Globochaete packestone with microfauna of *Lenticulina* sp., radiolarians, ostracods, "filaments" of juvenile bivalves and crinoids. Its uppermost part, belonging to the mid-Tithonian Chitinoidella Zone contains *Chitinoidella boneti, Ch. slovenica, Schizosphaerella minutissima, Cadosina fusca fusca, Colomisphaera carpathica,* phosphatized fish teeth, aptychi, crinoid columnalia, radiolarians and foraminifers, as well (Fig. 5).
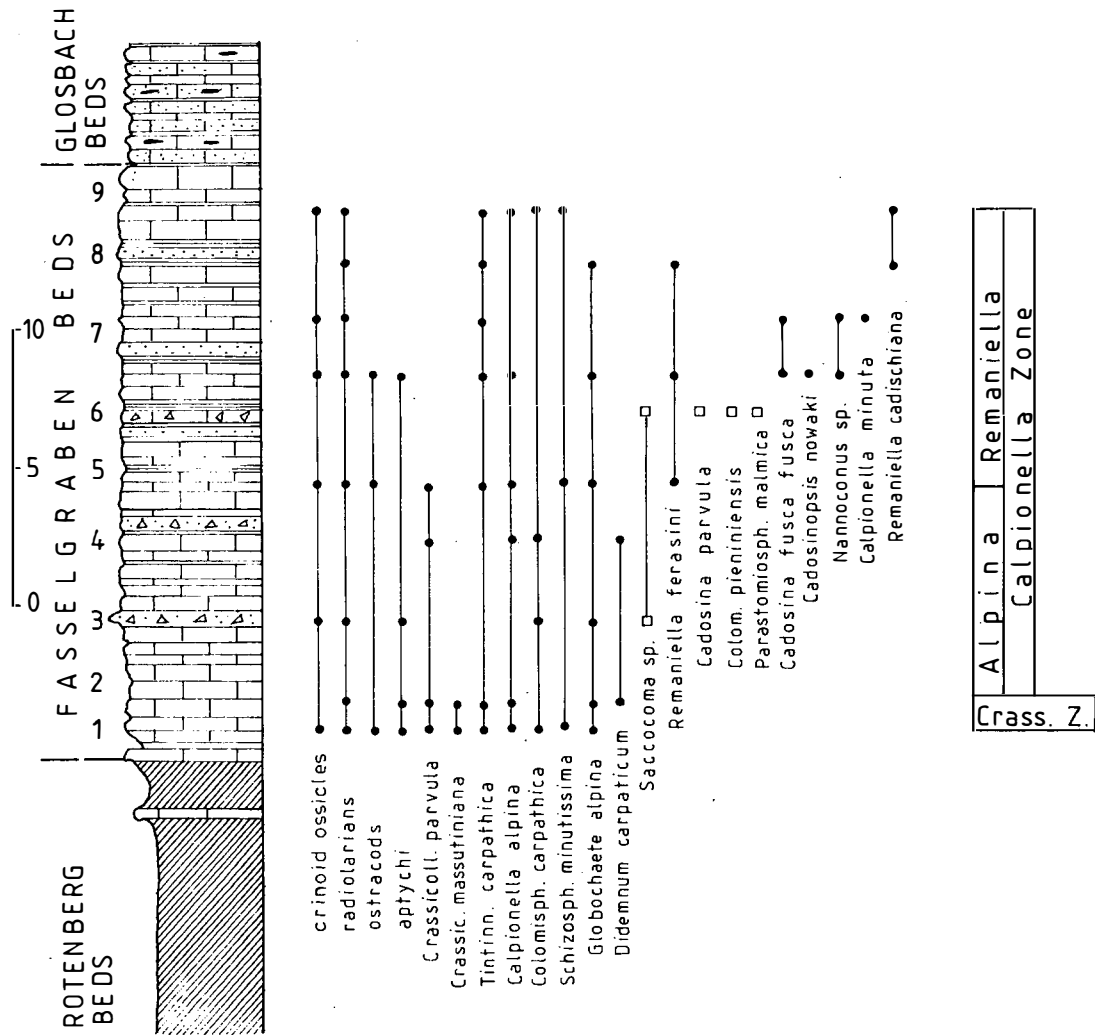
Fig. 4: Microbiostratigraphic evaluation of the Reidl section, Ybbsitz Klippen Belt, Penninic, Eastern Alps.

b. Crassicollaria-Globochaete wackestone of the late Tithonian Crassicollaria Zone encloses *Crassicollaria brevis, Cr. colomi, Cr. parvula, Calpionella alpina, Globochaete alpina, Tintinnopsella carpathica,* aptychi, crinoid columnalia and foraminifers.

c. Lower Berriasian Calpionella wackestone with *Tintinnopsella carpathica, Calpionella alpina, C. elliptica, Remaniella ferasini, R. filipescui, R. cadischiana* (COLOM), *Globochaete alpina, Schizosphaerella minutissima, Lenticulina* sp., radiolarians and crinoids pass upwards into bio-

micrite with less abundant microfossil association of the late Berriasian Calpionellopsis Zone (Pl. 1) *C. simplex, C. oblonga, T. carpathica, R. cadischiana, R. borzai* POP, *Cadosina fusca fusca, Calpionella alpina, Globochaete alpina, Textularia* sp., crinoids and foraminifers.

Thin-bedded gray-spotted marly limestone with laminae and intercalation of marl belongs to the Schrambach Formation. Nannoconid and radiolarian-nannoconid wackestone to mudstone contains *Colomisphaera heliosphaera, Col. lucida, Col. vogleri, Cadosina fusca fusca, Stomio-*

STEIN | SCHRAMBACH
KLAUS Lst | MÜHL Lst. | Lst. | T A N N H E I M   B E D S
VILS Lst

bryozoans
foraminifer fragments
crinoid oscicles
sponge spicules
ammonites
aptychi
globochaetes
radiolarians
ostracods

Colomisphaera fibrata
Didemnoides moreti
Saccocoma sp.
Chitinoidella boneti
Didemnum carpaticum
Colomisphaera tenuis
Colomisphaera carpathica
Cadosina minuta
Crassicollaria brevis
Crassicollaria parvula
Tintinnopsella doliphormis
Calpionella alpina
Remaniella ferasini
Tintinnopsella carpathica
Remaniella filipescui
Remaniella cadischiana
Calpionella elliptica
Calpionellopsis simplex
Calpionellopsis oblonga
Tintinnopsella longa
Cadosina fusca fusca
Nannoconus sp.
Stomiosphaera echinata
Colomisphaera vogleri
Stomiosphaera wanneri
Colomisphaera lucida
Colomisphaera heliosphaera
Globuligerina hoterivica
Hedbergella sigali
Textularia sp.
Martinotiella jucunda
Globigerinelloides blowi
Tincinella bejaouensis
Hedbergella globigerinelloides
Whiteinella sp.

Radiolarians

Acanthocircus dicranacanthos
Acanthocircus trizonalis
Acaeniotyle diaphorogona
Acaeniotyle umbilicata
Alievium helenae
Angulobracchia ? portmanni
Archaeodictyomitra lacrimula
Cecrops septemporatus
Crucella sp.
Neotripocyclia echiodes
Paronaella ? spinosa
Pseudocrucella procera
Pseudodictyomitra puga
Sethocapsa leiostraca
Sethocapsa trachyostraca
Sethocapsa uterculus
Thanarla sp.
Ultranapora cf. dumitricai

Chitinoidella Z.	Crassicollaria Z.	Calpionella Z.	Calpionellopsis Z.	Tintinnopsella Z.	Globuligerina hoterivica	Hedbergella sigali	Globigerinelloides blowi	Ticinella bejaouensis

Fig. 5: Microbiostratigraphic evaluation of the Hohenberg section, Frankenfels Nappe of the Bajuvaric, Northern Calcareous Alps.

sphaera wanneri, Tintinnopsella carpathica, T. longa, radiolarians (Pl. 2)*, Acanthocircus dicranacanthos* (SQUINABOL), *A. trizonalis* (RÜST), *Acaeniotyle diaphorogona* FOREMAN, *Ac. umbilicata* (RÜST), *Alievium helenae* SCHAAF, *Angulobracchia* (?) *portmanni* BAUMGARTNER, *Archaeodictyomitra lacrimula* (FOREMAN), *Cecrops septemporatus* (Parona), *Crucella* sp., *Suna echiodes* (FOREMAN), *Paronaella* (?) *spinosa* (PARONA), *Pseudocrucella procera* OŽVOLDOVÁ, *Crucella lipmanae* JUD, *Sethocapsa leiostraca* FOREMAN, *S. trachyostraca* FOREMAN, *S. uterculus* (PARONA), *Ultranapora* cf. *dumitricai* PESSAGNO, *Wrangelium medium* WU, ostracods and sponge spicules. Clastic admixture is represented by quartz grains and muscovite flakes. Calpionellids disappear upwards, being substituted by the planktonic foraminifers *Globuligerina hoterivica* and *Hedbergella sigali.*

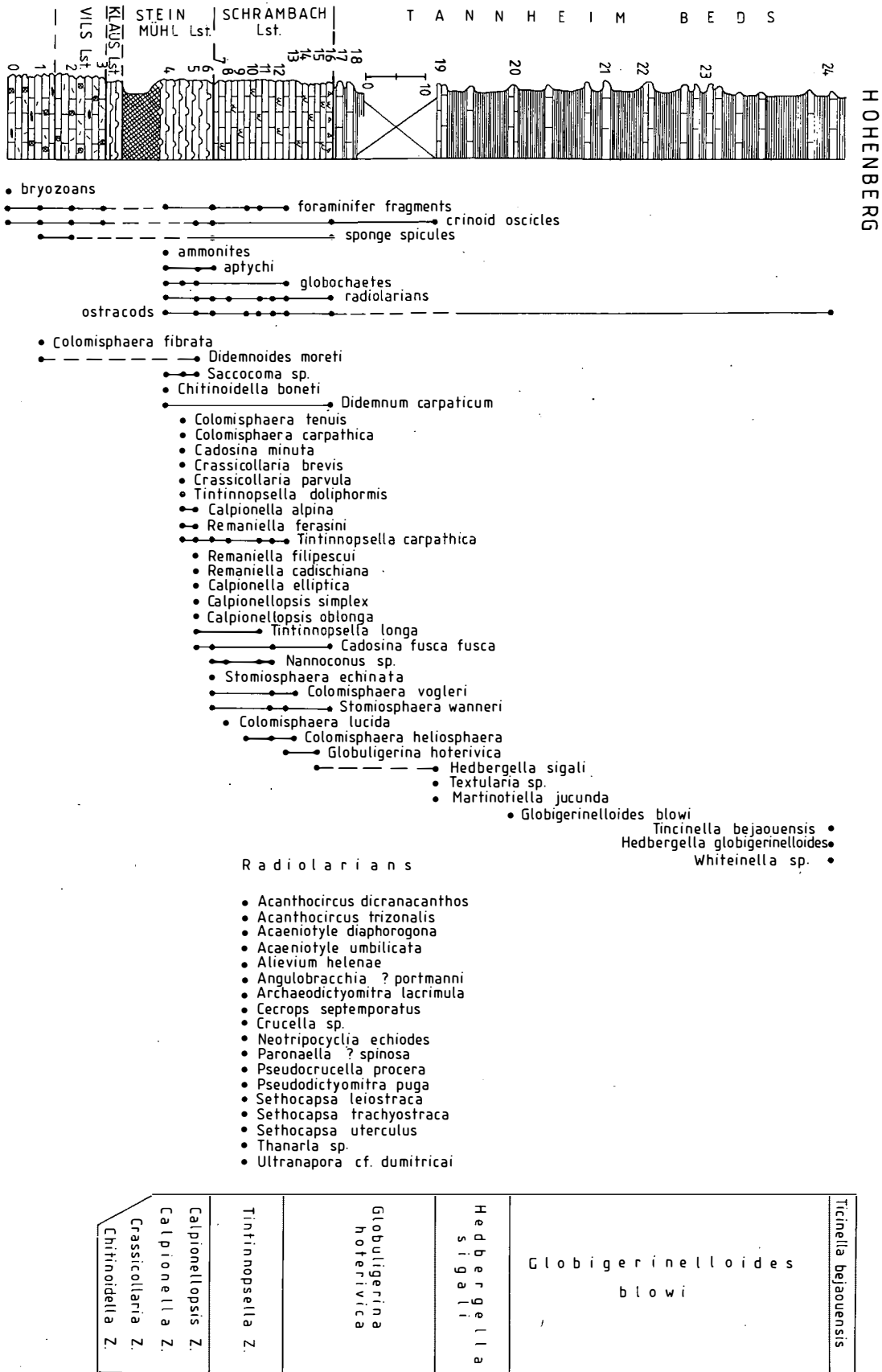Aptian association of planktonic foraminifers belonging to the Globigerinelloides blowi Zone (Pl. 3) was documented in a black marly complex with limestone intercalations (Tannheim Formation). A sample with early Albian plankton foraminifer association *Hedbergella globigerinelloides, Ticinella* sp. and *Whiteinella* sp. has been taken from the top part of the sequence.

2.2.2. Lunz Nappe (G. Flösselberg section)

Pink to pale brown micritic Steinmühl Limestone is characterized by Calpionella-radiolarian to radiolarian wackestone texture. It contains the microfossil association of the Remaniella Subzone (Fig. 6, Pl. 4): *Calpionella alpina, Tint. carpathica, Remaniella cadischiana, Rem. ferasini, Crassicollaria parvula, Cr. colomi, Nannoconus* sp., *Globochaete* sp., foraminifers, aptychi fragments and bivalves.

The Schrambach Formation consists of a rhythmic sequence of gray-spotted marly limestones (biomicritic mudstone to wackestone). VAŠÍČEK et al. (in print) described the microfossil association of the Tintinnopsella Zone from this section: *Tintinnopsella carpathica, Tintin. subacuta* (COLOM), *Cadosina semiradiata semiradiata, C. semiradia-*

ta cieszynica NOWAK, *C. semir. olzae* NOWAK, *C. fusca fusca, Colomisphaera vogleri, Cadosinopsis nowaki* BORZA, *Stomiosphaera echinata* NOWAK, *St. wanneri, Carpistomiosphaera valanginiana* BORZA, *Didemnoides moreti, Globochaete alpina* with abundant nannoconids, radiolarians, foraminifers, aptychi fragments, crinoids, ostracods. This micro- and macrofossil (ammonites, aptychi) association indicates early Hauterivian age.

The formation comprises several fine-grained detrital limestone beds of fluxoturbidite origin. They are built of siliceous bioclastic packestone with mass accumulation of sponge spicules, accompanied by *Cadosina fusca cieszynica,* radiolarians, foraminifers and crinoid columnalia. Clasts of biomicrite wackestone with *Calpionella alpina* occur sporadically. Clastic quartz and glauconite grains are frequent, being accompanied by less abundant mica flakes.

2.2.3. Reichraming Nappe (Anzenbach section)

Small quarry near the road from the Anzenbach Valley to Brennhöhe exposes upper member of the Schrambach Formation, built of dark gray marlstones/marly limestones. It yielded an early Hauterivian macrofauna of ammonites and belemnites (VAŠÍČEK et al., in print). Nannocone mudstone comprises microfossil association of the Tintinnopsella Zone: *Cadosina fusca fusca, Cad. semiradiata olzae, Stomiosphaera echinata, Tintinnopsella carpathica* (Pl.4).

2.3. Tirolic units

They represent the main structural element of the Northern Calcareous Alps (JANOSCHEK & MATURA, 1980). They comprise several partial tectonic units (Inntal-, Staufen-Höllengebirge-, Totes Gebirge-, Ötscher nappes). Upper Jurassic and Lower Cretaceous sedimentary record is represented by products of a basin (pelagite limestones of the Oberalm- and Schrambach formations; tur-
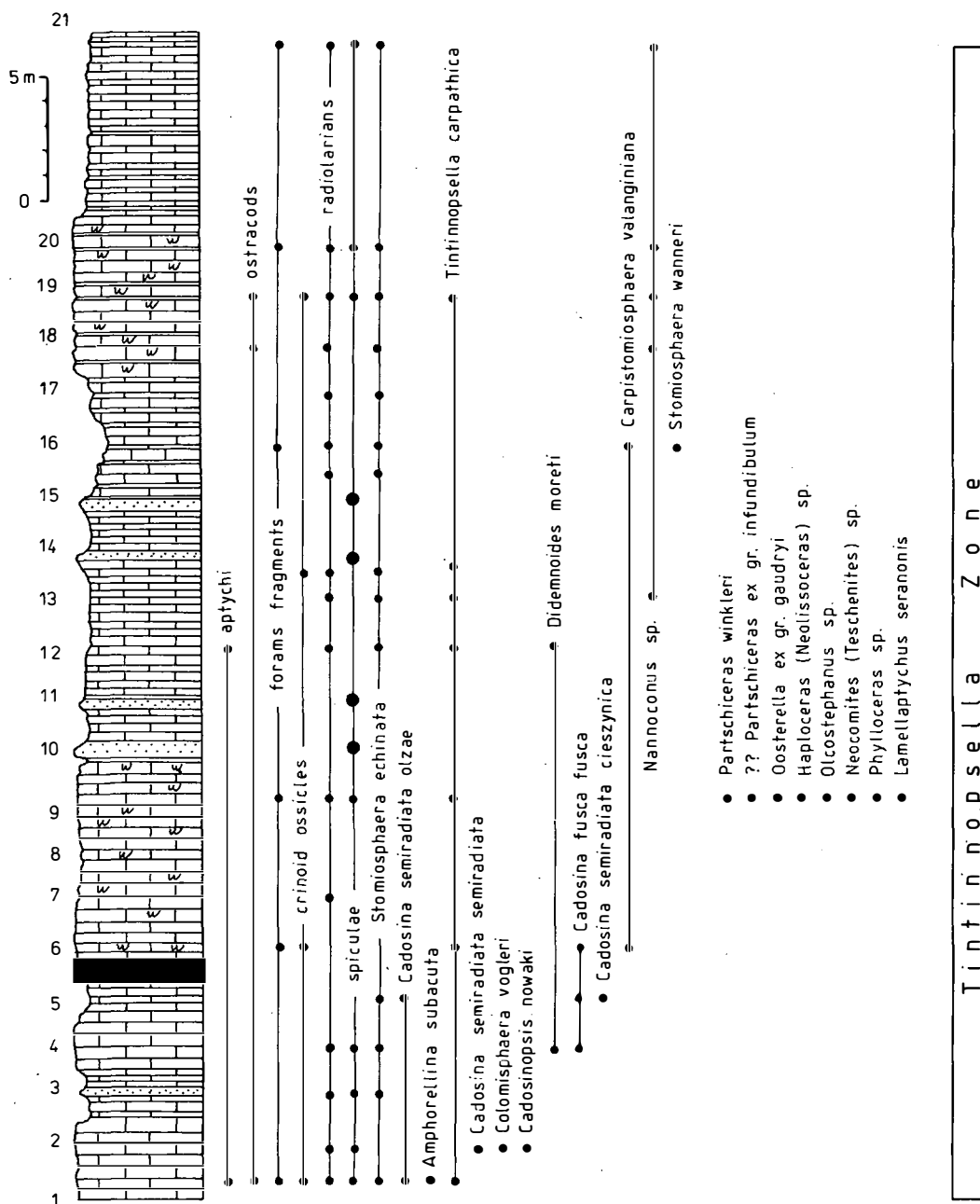
Fig. 6: Microbiostratigraphic evaluation of the Flössel section, Lunz Nappe of the Bajuvaric, Northern Calcareous Alps.

bidites of the Barmstein Formation) rimmed from the south and east by a shallow-marine carbonate platform (Plassenstein- and Tressenstein formations). During Hauterivian and Barremian the basin was filled by clastic sediments derived from emerging zones in the south (Roßfeld Formation).

2.3.1. Staufen-Höllengebirge Nappe (Gartenau section)

Well-bedded gray cherty micrites with aptychi fragments (Oberalm Fm) were interpreted as deep basinal deposits (FLÜGEL & FENNINGER, 1966).

They are characterized by Saccocoma wackestone structure with *Colomisphaera carpathica, Globochaete alpina,* foraminifers, ostracods and crinoid columnalia of Kimmeridgian age. Upwards, these rocks pass into Saccocoma-Globochaete wackestone (Pl. 4) with *Praetintinnopsella andrusovi* BORZA, *Colomisphaera carpathica* and radiolarians representing lower Tithonian strata. The topmost Crassicollaria-Globochaete wackestone with *Crassicollaria intermedia, Cr. parvula, Calpionella alpina, Tintinnopsella carpathica* accompanied by radiolarians (Pl. 5): *Acanthocircus dicranacanthos, Archaeodictyomitra apiaria, Emiluvia chica* FOREMAN, *Emiluvia ordinaria* OŽVOLDOVÁ, *Pantanellium squinaboli* (TAN), *Pseudodictyomitra carpatica* (LOZYNYAK), *Thanarla sp.* B. *Tritrabs ewingi* (PESSAGNO), foraminifers, crinoids, sponge sclerites and ostracods represents upper Tithonian. The Oberalm Formation contains calciturbidite layers of fine-detrital packestones and grainstones (Barmstein Fm).

FENNINGER & HOLZER (1972), relying on calpionellid zonation applied here by GARRISON (1967), regarded higher-lying well-bedded gray marly, locally bioturbated limestones with laminae or intercalations of marl as upper member of the Oberalm Beds. However, different lithology and microfauna of these beds lead us to the conclusion to consider them as part of the Schrambach Formation. It is represented by radiolarian wackestone and nannoconid mudstone. Dominating radiolarians *Archaeodictyomitra apiaria* (RÜST), *Archaeodictyomitra excellens* (TAN SIN HOK), *Holocryptocanium barbui* DUMITRICĂ, *Mirifusus dianae* (KARRER), *Pantanellium squinaboli* (PARONA), *Parvicingula cosmoconica* (FOREMAN), *Podobursa triacantha* (FISCHLI), *Pseudodictyomitra carpatica* (LOZYNYAK), *Sethocapsa* cf. *pseudouterculus* AITA, *Thanarla conica* (ALIEV), *Thanarla sp.* A, are accompanied by microfossils of Berriasian Calpionella- and Calpionellopsis Zones (Pl. 4): *Calpionella alpina, Tintinnopsella carpathica, Calpionella elliptica, Remaniella cadischiana, Calpionellopsis simplex, Cadosina fusca fusca, Schizosphaerella minutissima,* sponge spicules, ostracod tests, foraminifer fragments.

3. Discussion

Six sections representing Lower Cretaceous pelagic limestone sequences of selected units of the Eastern Alps have been evaluated microbiostratigraphically.

Majolica type limestones of the Penninic units (Texing section in the Gresten Zone; Reidl section in the Ybbsitz Zone) yielded rich associations of Berriasian calpionellid comparable with those in the Pieniny Klippen Belt of the Western Carpathians. The occurrence of limestone breccias in the southern Penninic Ybbsitz Zone is remarkable. They resemble the Nozdrovice Breccia, studied in the Western Carpathians by REHÁKOVÁ & MICHALÍK (1995). The clasts from this breccia were derived from underlying Upper Jurassic strata as well. However, in addition, they also contain abundant clastic quartz and glauconite grains, and even crystalline schist fragments, similar to equivalent breccias described by REHÁKOVÁ et al. (1995) from the Outer Carpathian Magura Basin, or by PLAŠIENKA et al. (1994) from the southern margin of the Penninic Basin in the Považský Inovec Mts (Central Western Carpathians).

The Hohenberg section (in the Frankenfels Nappe) well illustrates the persistence of limestone facies of the "Ammonitico Rosso" type (here represented by the Steinmühl Formation with Tithonian and Berriasian calpionellid associations) until the earliest Valanginian. Calpionellid loricas from these associations are larger and their excellent preservation proves more rapid lithification of the sediment if compared with their basinal counterparts. The persistence of Upper Jurassic elevation facies is unusual in the majority of Alpine and Carpathian Lower Cretaceous sequences. Noteworthy, a similar habitus of calpionellid loricas has been described in peripheral parts of the Fatric area in the central Western Carpathians by BORZA (1969, from the Manin Unit) or by MICHALÍK et al. (1994, MLS-1 borehole, northern margin of the Humenné Mts).

The Valanginian-Hauterivian part of the Lower Cretaceous pelagic sequence of the Frankenfels Nappe is represented by the basinal Schrambach Formation. In several units of the Bajuvaric
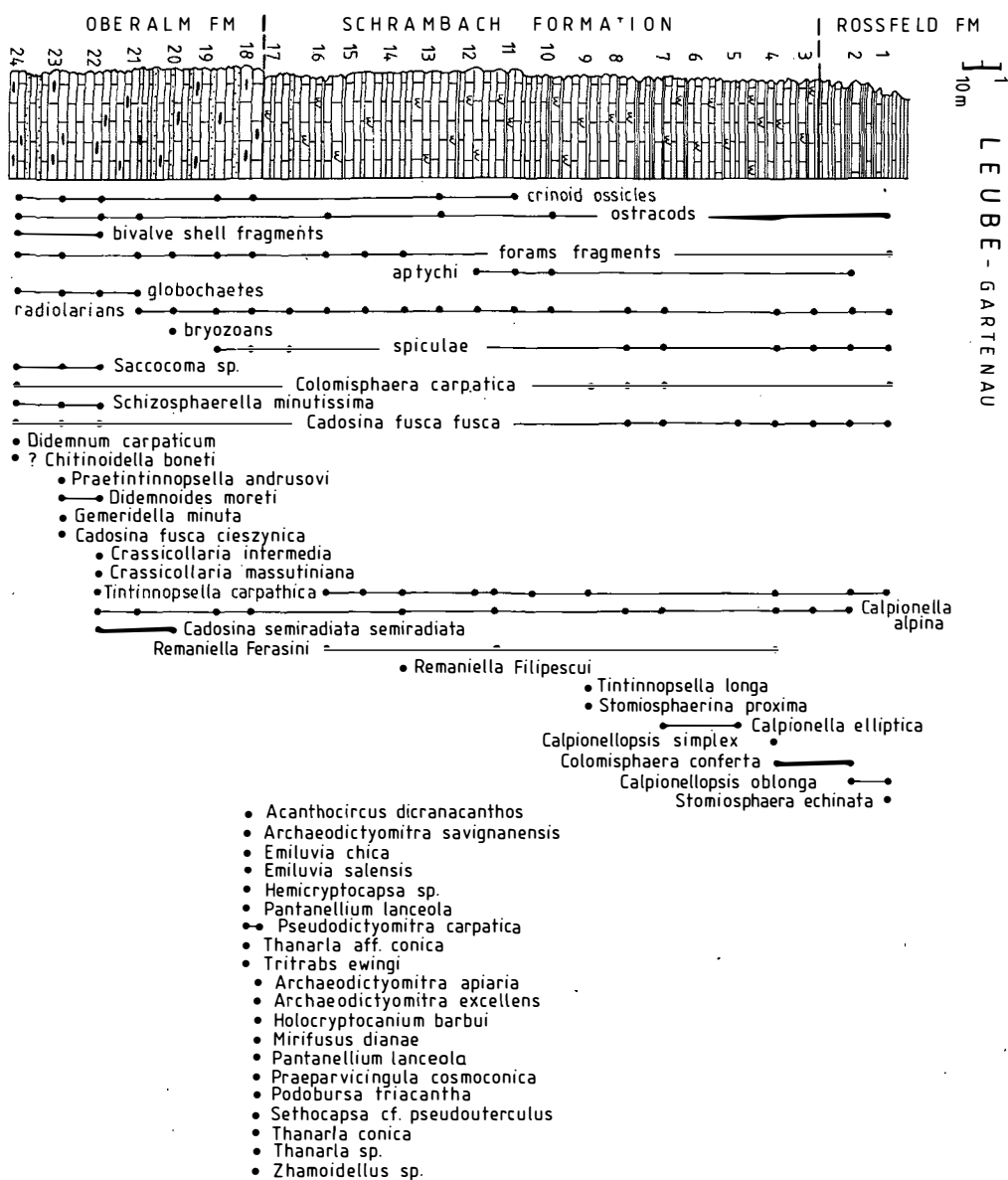
Fig. 7: Microbiostratigraphic evaluation of the Gartenau section, Staufen-Höllengebirge Nappe of the Tirolic, Northern Calcareous Alps.

(Lunz-, Reichraming Nappes) and of the Tirolic (Staufen-Höllengebirge Nappe), basinal development started as early as in the Berriasian. Besides calcareous microplankton, stratigraphically important ammonites and radiolarians helped to establish the age of this formation. *Cecrops septem-poratus* and *Crucella lipmanae* indicate late Valanginian to early Hauterivian age of the radiolarian association (cf. BAUMGARTNER, 1984, 1987; JUD, 1994; GORIČAN, 1994), occurring in the Schrambach Formation of the Hohenberg section (Bed No. 9; Fig. 5, Pl. 2) along with calcareous mi-

croplankton of the Tintinnopsella Zone. Early Hauterivian age of the Schrambach Fm in the G. Flösselberg section is (besides microplankton of the Tintinnopsella Zone) also evident by finding of *Spitidiscus* sp. and *Lamellaptychus* cf. *serranonis* (VAšíČEK et al., 1994 a).

Occurrence of the radiolarian Unitary Association U.A. 11 (according to BAUMGARTNER, 1984, 1987) in the sample No. 18 from the Gartenau (Leube) section (Staufen Nappe of Tirolic) corresponds quite well to the lower Berriasian calpionellid association characterizing the Alpina Subzone.

If compared with the sample mentioned, the association of the Bed No. 17 (Fig. 7), although more abundant, comprises species with wider stratigraphic span. According to BAUMGARTNER (l.c.), *Holocryptocanium barbui* DUMITRICĂ should appear during the late Berriasian. However, it occurs in association of lower Berriasian calpionellids. A similar case (the occurrence of "stratigraphically younger" *Pseudodictyomitra lilyae* and *Archaeodictyomitra nuda* in the lower Berriasian association 11 U.A.) was recorded by ONDREJÍČKOVÁ et al. (1993).

Radiolarian biostratigraphic scale is still in progress now. We hope that new data on the stratigraphic range of radiolarian taxa from detailed Berriasian key sections supported by other index fossils will lead to a more precise view in proximal future.

4. Acknowledgements

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Authors' addresses:

RNDr. Jozef Michalík, DrSc. , RNDr. Daniela Reháková CSc., Geological Institute of the Slovakian Academy of Sciences, Dúbravská cesta 9, SK-842 26 Bratislava, Slovakia;
RNDr. Ladislava Ožvoldová, CSc., Comenius University, Faculty of Sciences, Department of Geology and Paleontology, Mlynská dolina G-1, SK-842 15 Bratislava, Slovakia.

Plate 1

Calcareous microplankton from the Steinmühl Formation in the Hohenberg section (Frankenfels Nappe of the Bajuvaric), Northern Limestone Alps. The specimens were derived from beds No 4 (Figs. 7–8, 10–11, 13), 5 (Fig. 12) and 6 (Figs. 1–6, 9). Magnification: 155 x (Figs. 1–3, 6, 10, 12) and 265 x (Figs. 4–5, 7–9, 11, 13), respectively.

Fig. 1:   *Textularia* sp.
Fig. 2:   *Permodiscus* sp.
Fig. 3:   *Calpionellopsis oblonga* (CADISCH)
Fig. 4:   *Calpionellopsis simplex* (COLOM)
Fig. 5:   *Remaniella filipescui* POP
Fig. 6:   *Calpionellopsis oblonga* (CADISCH)
Fig. 7:   *Colomisphaera carpathica* (BORZA)
Fig. 8:   *Chitinoidella boneti* DOBEN
Fig. 9:   *Tintinnopsella carpathica* (MURGEANU et FILIPESCU)
Fig. 10:   *Saccocoma* sp.
Fig. 11:   *Chitinoidella boneti* DOBEN
Fig. 12:   *Calpionella elliptica* CADISCH and *Tintinnopsella carpathica* (MURG. et FILIP.)
Fig. 13:   *Cadosina semiradiata* WANNER
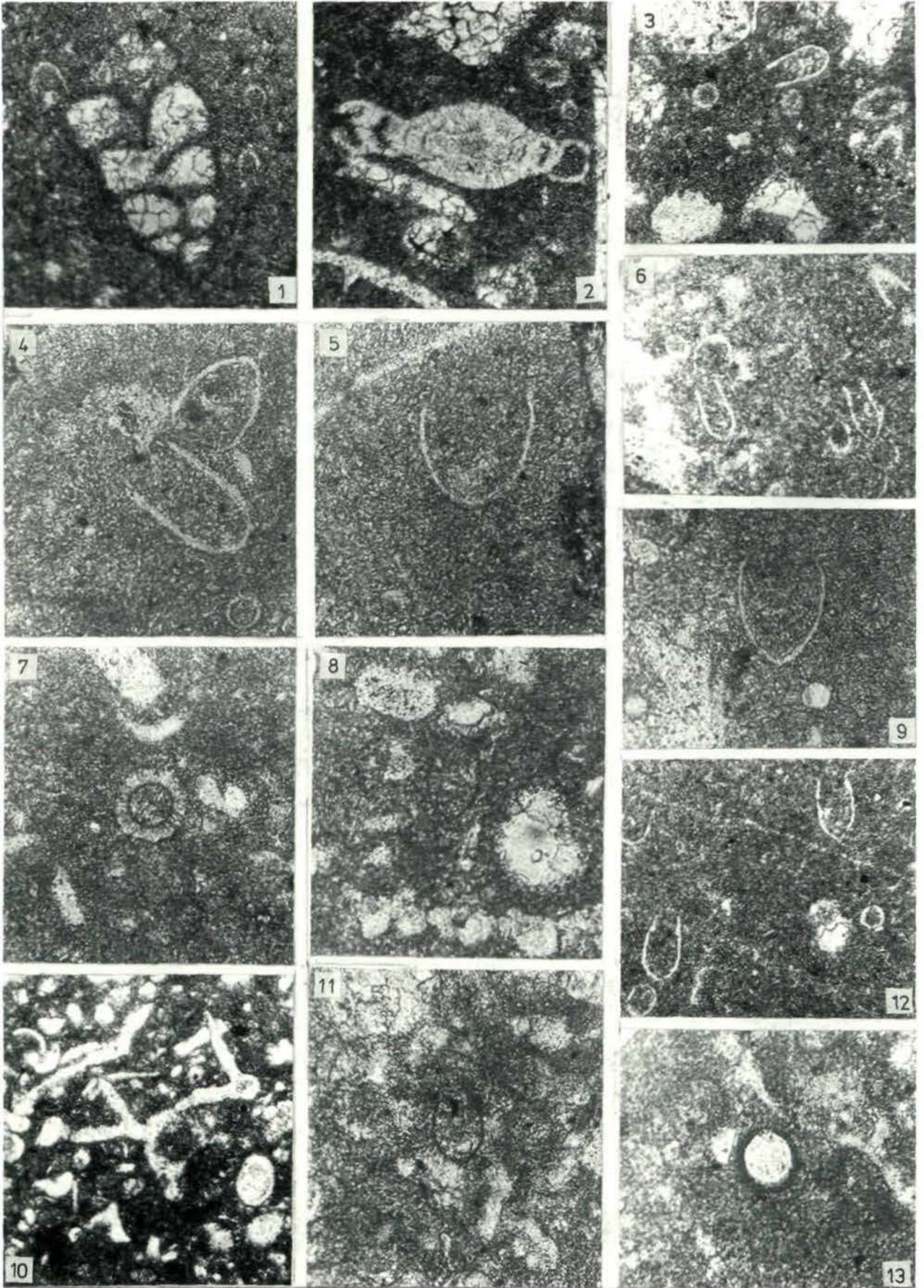
Plate 2

Radiolarian association from the Hohenberg section, Frankenfels Nappe of the Bajuvaric, Northern Limestone Alps, sample 21.

Fig. 1:   Foraminifer *Anomalinidae* gen. indet., 115 x
Fig. 2:   *Suna echiodes* (FOREMAN), 200 x
Fig. 3:   *Crucella lipmanae* JUD, 130 x
Fig. :   *Acanthocircus dicranacanthos* (SQUINABOL), 240 x
Fig. 5:   *Sethocapsa uterculus* (PARONA), 300 x
Fig. 6:   *Archaeodictyomitra lacrimula* (FOREMAN), 240 x
Fig. 7:   *Angulobracchia* (?) *portmanni* BAUMGARTNER, 150 x
Fig. 8:   *Wrangellium medium* WU, 280 x
Fig. 9:   *Pseudocrucella procera* OŽVOLDOVÁ, 175 x
Fig. 10:   *Alievium helenae* SchAAF, 195 x
Fig. 11:   *Ultranapora* cf. *dumitricai* PESSAGNO, 240 x
Fig. 12:   *Cecrops septemporatus* (PARONA), 215 x
Figs. 13,15: *Crucella* sp., 240 and 350 x, proximal and lateral view
Fig. 14:   *Paronaella* (?) *spinosa* (PARONA), 160 x
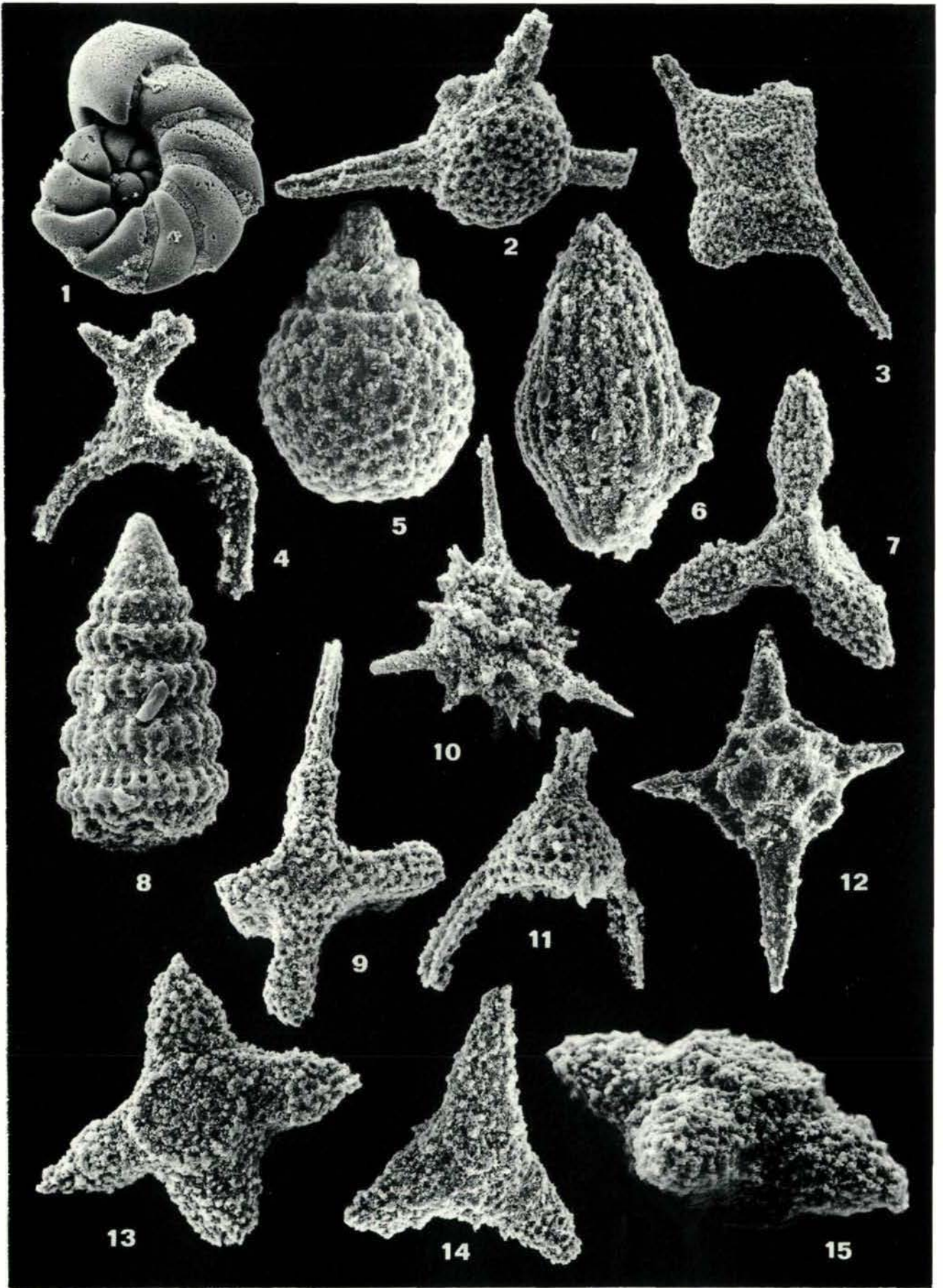
Plate 3

Calcareous microplankton from the Tannheim- (Figs. 1–4), Schrambach- (Figs. 5–15) and Oberalm (Figs. 16–19) formations in both the Hohenberg- (Frankenfels Nappe of Bajuvaric) and Gartenau (Staufen-Höllengebirge Nappe of the Tirolic) sections, Northern Limestone Alps. Magnification 155 (Fig. 5) and 265 x (Figs. 1–4, 6–19), respectively.

Fig. 1: *Hedbergella sigali* MOULLADE, Hohenberg No. 15

Fig. 2: *Globigerinelloides blowi* (BOLLI), Hohenberg No. 21

Fig. 3: *Hedbergella globigerinelloides* (SUBB.), Hohenberg No. 23

Fig. 4: *Ticinella sp.*, Hohenberg No. 24

Fig. 5: radiolarian wackestone, Hohenberg No. 9

Fig. 6: *Tintinnopsella carpathica* (MURG. et FIL.) Hohenberg No. 11

Fig. 7: *Calpionella elliptica* CADISCH, Gartenau No. 7

Fig. 8: *Schizosphaerella minutissima* (COLOM), Gartenau No. 7

Fig. 9: *Colomisphaera heliosphaera* (VOGLER), Hohenberg No. 14

Fig. 10: *Colomisphaera vogleri* (BORZA), Hohenberg No. 11

Fig. 11: *Stomiosphaera wanneri* BORZA, Hohenberg No. 23

Fig. 12: *Calpionella alpina* LORENZ, Gartenau No. 2

Fig. 13: *Calpionella elliptica* CADISCH, Gartenau No. 4

Fig. 14: *Remaniella cadischiana* (COLOM), Gartenau No. 4

Fig. 15: *Cadosina semiradiata semi radiata* WANNER and *Cadosina fusca fusca* WANNER, Gartenau No. 1

Fig. 16: *Praetintinnopsella andrusovi* BORZA, Gartenau No. 23

Fig. 17: *Crassicollaria intermedia* (DUR. DELGA), Gartenau No. 22,

Fig. 18. *Schizosphaerella minutissima* (COLOM), Gartenau No. 22

Fig. 19: *Colomisphaera carpathica* (BORZA), Gartenau No. 24
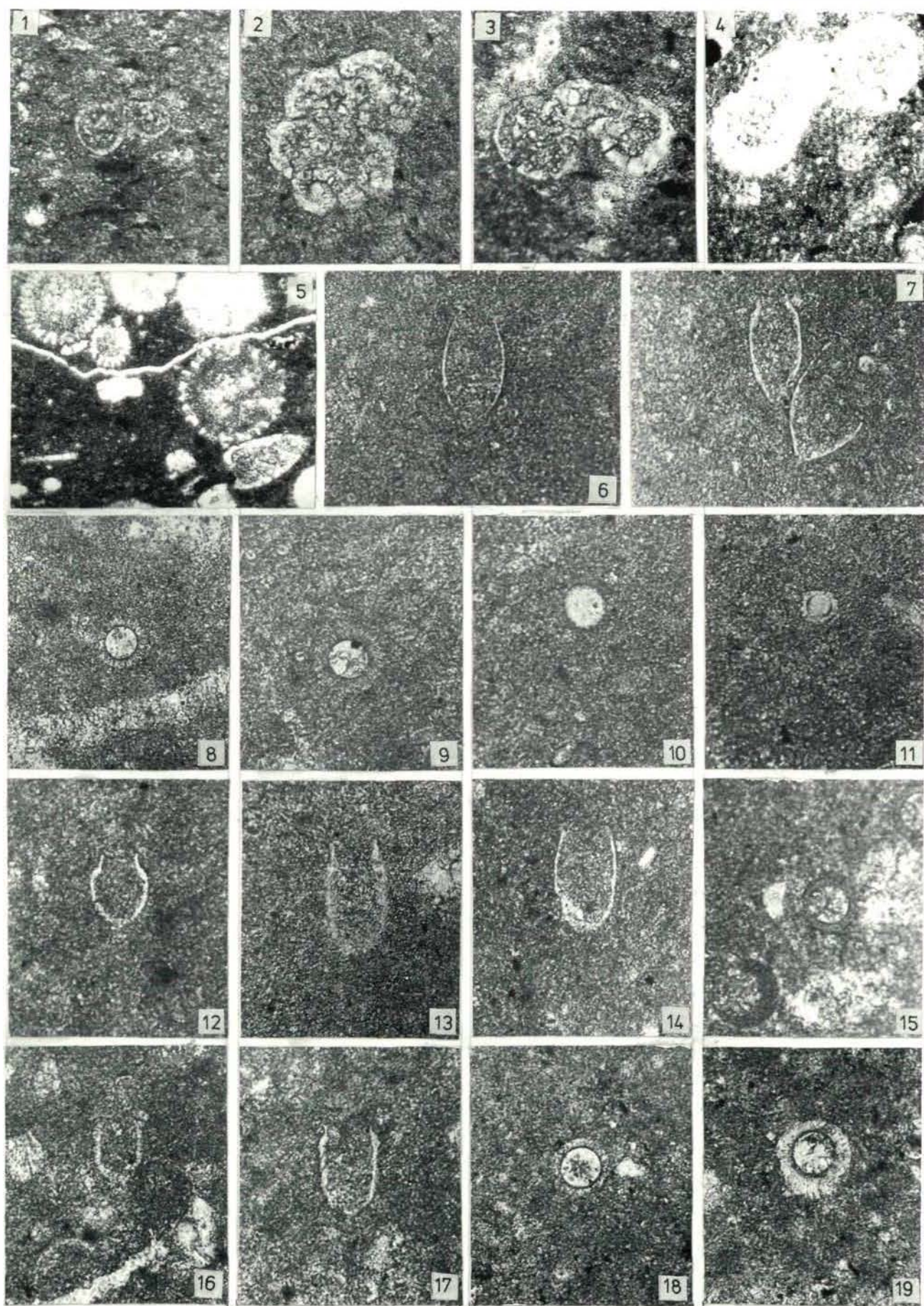
Plate 4

Calcareous microplankton from the Schrambach Formation, Lunz (G. Flösselberg section, Figs. 2–3, 5–13), and Reichraming (Anzenbach section, Figs. 1,4) nappes of the Bajuvaric, Northern Limestone Alps. Magnification 265 x.

Figs. 1–2:   *Cadosina fusca fusca* WANNER
Fig. 3:   *Schizosphaerella minutissima* (COLOM)
Figs. 4–5:   *Cadosina semiradiata olzae* NOWAK
Fig. 6:   *Cadosinopsis nowaki* BORZA
Fig. 7:   *Colomisphaera conferta* ŘEHÁNEK
Fig. 8:   *Colomisphaera vogleri* (BORZA)
Fig. 9:   *Carpistomiosphaera valanginiana* BORZA
Fig. 10:   *Stomiosphaera echinata* NOWAK
Figs. 11–12: *Tintinnopsella carpathica* (MURGEANU et FILIPESCU)
Fig. 13:   *Remaniella borzai* POP
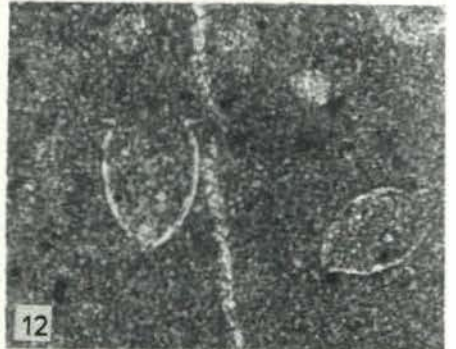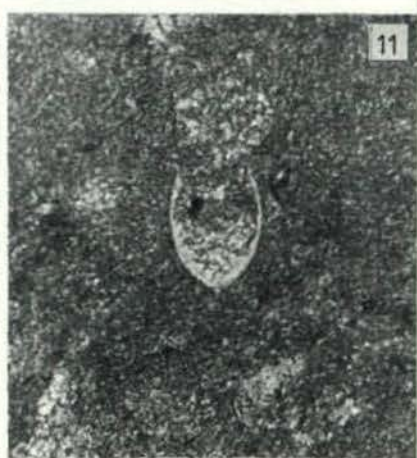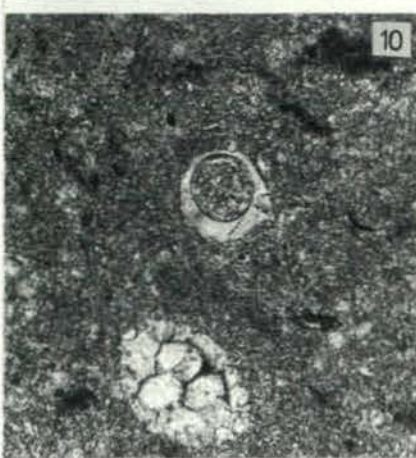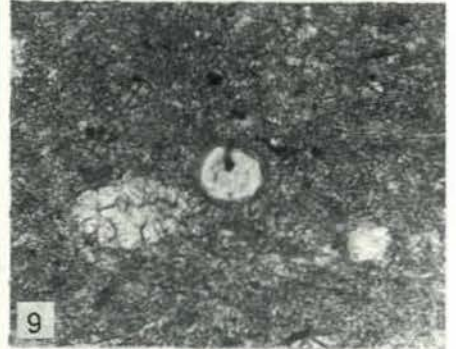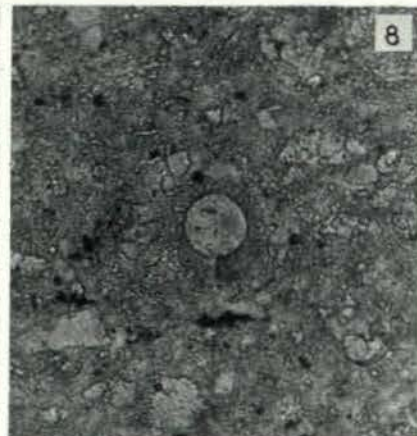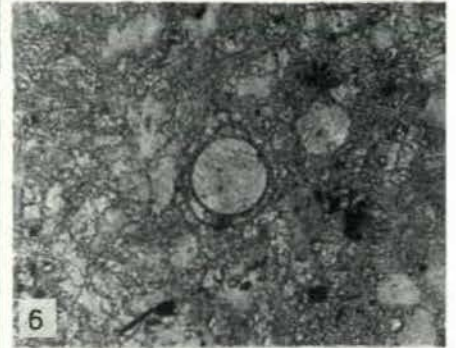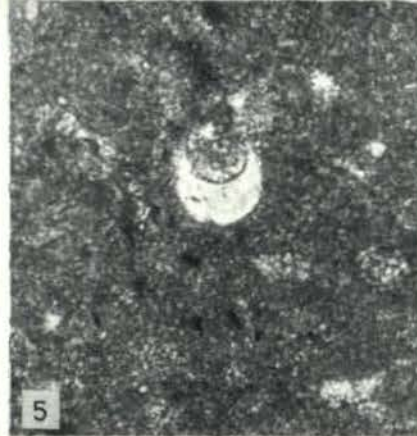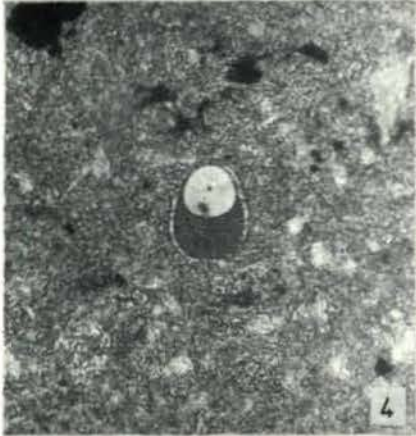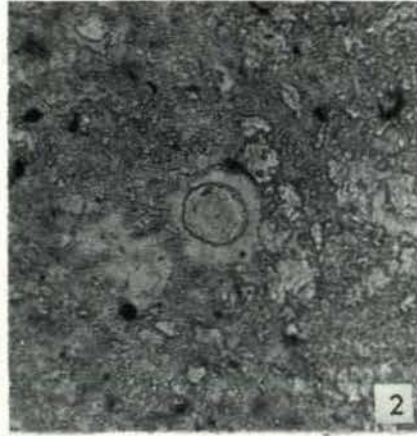
Plate 5

Late Tithonian / Berriasian radiolarian association from the Gartenau (Leube) section, Staufen-Höllengebirge Nappe of the Tirolic, Northern Limestone Alps. Specimens 1–4, 9–10, 15 came from sample L-18, specimens 5–8, 11–14 were yielded from sample L-17.

Fig. 1:   *Archaeodictyomitra apiaria* (Rüst), 450 x
Fig. 2:   *Pseudodictyomitra carpatica* (Lozynyak), 280 x
Fig. 3:   *Emiluvia ordinaria* Ožvoldová, 200 x
Fig. 4:   *Thanarla conica* (Aliev), 400 x
Fig. 5:   *Thanarla* sp. A, 400 x
Fig. 6:   *Sethocapsa* cf. *pseudouterculus* Aita, 300 x
Fig. 7:   *Parvicingula boesii* (P), 300 x
Fig. 8:   *Archaedictyomitra exceltens* (Tan Sin Hok), 240 x
Fig. 9:   *Pantanellium squinaboli* (Tan), 300 x
Fig. 10: *Thanarla* sp. B., 300 x
Fig. 11: *Parvicingula cosmoconica* (Foreman), 330 x
Fig. 12: *Pseudodictyomitra carpatica* (Lozynyak), 300 x
Fig. 13: *Archaedictyomitra apiaria* (Rüst), 280 x
Fig. 14: *Holocryptocanium barbui* Dumitrică, 280 x
Fig. 15: *Emiluvia chica* Foreman, 160 x

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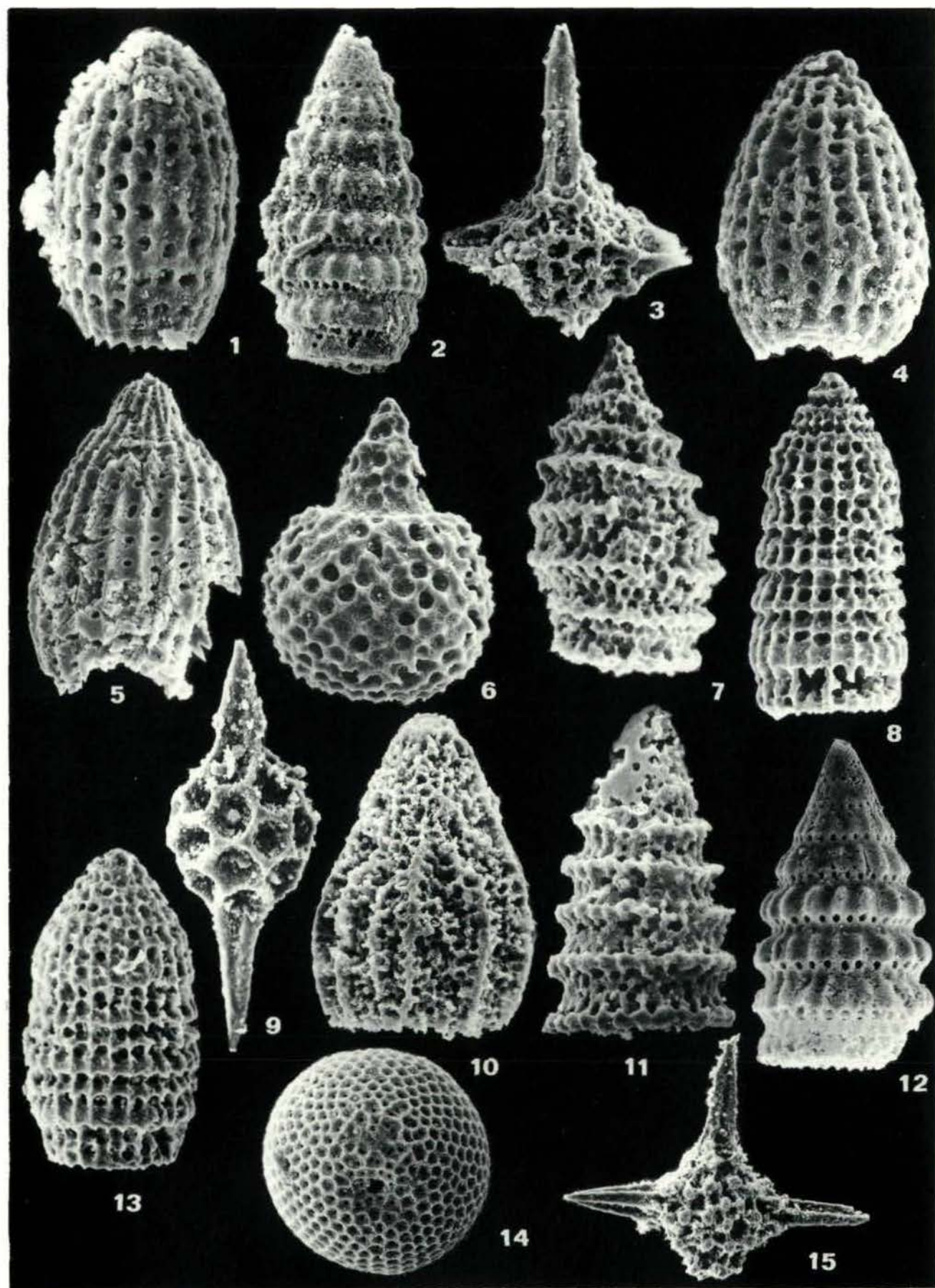
LONGOBARDIAN (LATE LADINIAN) MUELLERITORTIIDAE (RADIOLARIA) FROM THE REPUBLIC OF BOSNIA-HERCEGOWINA

Heinz Kozur & Helfried Mostler

With 2 figures and 3 plates

Abstract:
Muelleritortiidae are common in radiolarian faunas of the Longobardian *Budurovignathus mungoensis* conodont zone from the locality Varoski Creek near Fojnica south of Sarajevo. *Muelleritortis,* among them the Longobardian index species *M. cochleata* (Nakaseko & Nishimura), clearly dominate over *Pentatortis* and primitive *Tritortis* species. 10 new species and subspecies are described.

Zusammenfassung:
Muelleritortiidae treten in longobardischen Radiolarien-Faunen aus der *Budurovignathus mungoensis*-Conodontenzone der Lokalität Varoski-Bach bei Fojnica südlich Sarajevo häufig auf. *Muelleritortis,* darunter die longobardische Index-Art *M. cochleata* (Nakaseko & Nishimura) dominieren bei weitem gegenüber *Pentatortis* und primitiven *Tritortis*-Arten. 10 neue Arten und Unterarten werden beschrieben.

1. Introduction

Muelleritortiidae belong to the stratigraphically most important and world-wide distributed Triassic radiolarians. They are restricted to the Longobardian to Cordevolian interval, where they often clearly dominate over other radiolarians. The maximum diversity is in the middle and late Longobardian. In addition to previously described species, several new taxa of Muelleritortiidae have been found in the Longobardian of Bosnia-Hercegowina that are described in the present paper.

The material was derived from the locality Varoski Creek, about 2 km west of Fojnica at the road Mostar-Gacko (Geological Map 135 Gacko 1:50 000) south of Sarajevo (Republic Bosnia-Hercegowina). The locality data were published by Murgenovic & Gaković, 1964. The material was sampled by L. Krystyn (Vienna). The radiolarians were derived from a micritic limestone (sample 88-272 of Krystyn's collection) with an inter-

calation of tuffitic claystones and radiolarite. The Longobardian age was determined by radiolarians of the of lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian). *Budurovignathus mungoensis* (Diebel), the conodont index species of the middle to late Longobardian *B. mungoensis* Zone is also present, but very rare.

2. Systematic part

All figured material is frosm radiolarian-bearing micritic limestones of the locality Varoski Creek. The limestone was a floated block. Therefore it is not clear, whether it was derived from below or above the tuffitic claystones-chert intercalation. The material is deposited in the Institute of Geology and Paleontology, Innsbruck University.

Fig. 1: Locality map. a) Geographic position of the locality (asterisk) in the Republic Bosnia-Hercegowina. b) Detailed locality map from MUDRENOVIĆ & GAKOVIĆ (1964).

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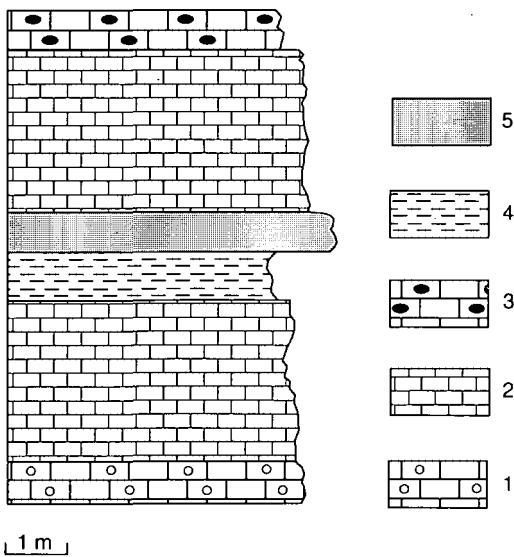
Fig. 2: Lithostratigraphic sequence with radiolarian-bearing limestone below and above a thin radiolarite-tuffit intercalation (from MUDRENOVIĆ & GAKOVIĆ, 1964). Vertical scale indicated.

1 = Calcarenite
2 = radiolarian-bearing limestone
3 = cherty limestone with *Joannites klipsteini* and *J. cymbiformis*
4 = tuffitic claystones
5 = red radiolarite

Subclass Radiolaria MÜLLER, 1858
Order Polycystina EHRENBERG, 1838
Suborder Entactinaria KOZUR & MOSTLER, 1982
Superfamily Palaeoscenidiacea RIEDEL, 1967

Family Muelleritortiidae KOZUR, 1988

Description: Thick-walled, two-layered shell spherical, subspherical or with subtriangular, triangular, subquadratic to quadratic outline in polar view (perpendicular to the equatorial plane of main spines). Inner layer with small pores. Outer layer consisting of pore frames with large, polygonal or roundish pores that differ in size and outline. The pore frames are often high and rather broad, mostly with nodes on the vertices. Sometimes the pore frames of the outer layer are low, rarely indistinct and absent near the equatorial margin of the main spine plane. Exceptionally the outer layer is very indistinct or even absent. Very rarely the co-

arse outer pore frames are partly covered by a spongy layer.

There are 2–6, mostly 3 or 4 main spines with 3 rounded, very broad ridges, which are subdivided by a deep and mostly broad distinct furrow which may be nearly as wide as the furrows between the ridges. By this the main spines appear often hexacarinate. Independent from the number of the main spines, always one of them display straight ridges, whereas the remaining 1–5 main spines displays twisted ridges. The main spines are mostly situated in the equatorial plane, but in few taxa a part of the twisted main spines runs oblique to the equatorial plane.

The inner structure is known only from *Muelleritortis*. It consists of a modified pentactine spicular system situated perpendicularly to the equatorial plane. The 3–4 apical spines are connected with the outer shell, but do not continue beyond the shell. The 4 basal spines are connected with the 4 main spines. Between the 4 basal spines arches are present which are also connected with the ridges of the main spines. Between these arches a coarse lattice is present which built up a loose medullary shell. Antapical this medullary shell is connected by a bunch of at least 4 spines with the outer shell. Further connecting spines between the medullary shell and the outer shell may be present. All these spines do not continue beyond the outer shell. Often the lattice of the medullary shell is not preserved. In this case only the apical and basal spines and the arches between the latter ones are present. If also the arches are broken away and only the apical and basal spines are preserved, the spicular system is similar to a strongly asymmetrical hexastylacean spicular system.

Occurrence: Longobardian to Cordevolian. Very common in the Tethys, but also present in the Circum-Pacific realm (Japan, Philippines and western Canada).

Assigned genera:
Muelleritortis KOZUR, 1988
Ditortis KOZUR, 1988
Pentatortis KOZUR, 1988
Tritortis KOZUR, 1988
Remarks: The Muelleritortiidae KOZUR, 1988, evolved from the Sepsagonidae KOZUR & MOST-

LER, 1981, that have the same inner structure and a similar structure of the two-layered cortical shell. However, in the Sepsagonidae are all main spines are either twisted or untwisted. The combination of one untwisted with 1-5 twisted main spines is unique and characteristic for the Muelleritortiidae. Despite the different morphology, mainly caused by the different number and arrangement of the main spines (2–6), the combination of one untwisted and 1–5 twisted main spines indicates that the Muelleritortiidae are a closely related group.

Genus *Muelleritortis* KOZUR, 1988

Type species: *Emiluvia* (?) *cochleata* NAKASEKO & NISHIMURA, 1979
Description: With the character of the family. Cortical shell spherical, subspherical or in polar view with subquadratic to quadratic outline. Four main spines, mostly in cross-like arrangement. Exceptionally the three twisted main spines may be in subpolar arrangement. The untwisted main spine is often longer than the twisted main spines.
Assigned taxa:
Muelleritortis cochleata cochleata NAKASEKO & NISHIMURA, 1979
Muelleritortis cochleata minoense NAKASEKO & NISHIMURA, 1979
Synonym: *Muelleritortis cochleata hungarica* DOSZT & LY, 1991
Muelleritortis cochleata koeveskalensis KOZUR, 1988
Muelleritortis cochleata tumidospina KOZUR, 1988
Muelleritortis longispinosa KOZUR, 1988
Muelleritortis pulchra pulchra KOZUR, 1988
Muelleritortis pulchra rotunda n. subsp.
Muelleritortis bosniensis n. sp.
Muelleritortis expansa n. sp.
Muelleritortis quadrata quadrata n. sp.
Muelleritortis quadrata parvispina n. subsp.
Muelleritortis ? *firma* (GORIČAN in GORIČAN & BUSER, 1990)
Synonym: *Muelleritortis nobilis* DOSZT & LY, 1991

Occurrence: Rare in the early Longobardian (only forms with untwisted or very slightly twisted main spines). Common in the middle and late Longobardian, very rare in the basal Cordevolian. Tethys, Philippines, Japan, British Columbia.

Remarks: The other Muelleritortiidae are distinguished by the number of arrangement of main spines (2 polar main spines in *Ditortis*, 3 main spines in triangular or subpolar arrangement in *Tritortis*, 5-6 main spines in *Pentatortis*).

In *Muelleritortis* ? *firma* (GORIČAN in GORIČAN & BUSER, 1990) all 4 main spines are untwisted. However, in some specimens (e.g. GORIČAN & BUSER, 1990, pl. 6, fig. 5) 3 main spines are very slightly twisted, the fourth one is untwisted. Similar or identical forms with one untwisted and 3 very slightly twisted main spines occur in the early Longobardian *Budurovignathus hungaricus* conodont zone of Hungary and in the lower subzone (*Pterospongus alatus* Subzone) of the Muelleritortiidae Zone of Hungary and Southern Alps. They may represent the long-ranging forerunner of typical *Muelleritortis* with one straight and 3 strongly twisted main spines.

Muelleritortis cochleata
(NAKASEKO & NISHIMURA, 1979)
(Pl. 1, Figs. 6, 7, 9, 10;
Pl. 2, Figs. 1, 4, 8; l. 3, Figs. 1, 3)

1979 *Emiluvia* (?) *cochleata* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 70, Pl. 3, Figs. 2–4, 6

1979 *Staurocontium minoense* NAKASEKO and NISHIMURA, n. sp., pars – NAKASEKO & NISHIMURA, p. 71, Pl. 2, Figs. 7, 9, 10; non! Pl. 12, Fig. 4

1984 *Plafkerium* sp. – DE WEVER, Pl. 3, Fig. 10

1986 *Emiluvia* (?) aff. *cochleata* NAKASEKO & NISHIMURA-BRAGIN, Pl. 2, Fig. 8

1988 *Muelleritortis cochleata cochleata* (NAKASEKO & NISHIMURA, 1979) – KOZUR, p. 53, Pl. 1, figs. 1–8; Pl. 2, Figs. 1, 2; Pl. 3, Fig. 1

1988 *Muelleritortis cochleata koeveskalensis* n. subsp. – KOZUR, p. 53–54, Pl. 3, Fig. 3

1988 *Muelleritortis cochleata tumidospina* n. subsp. - KOZUR, p. 54, Pl. 3, Fig. 2

1988 *"Emiluvia" cochleata* NAKASEKO ; NISHIMURA-BRAGIN, PL. 2, Fig. 8

1989 *Plafkerium cochleata* (NAKASEKO & NISHIMURA) – DOSZT & LY, Pl. 2, Figs. 1-3

1990 *Plafkerium* sp. -GORICAN & BUSER, p. 153, Pl. 6, Fig. 9

1991 *Muelleritortis cochleata cochleata* (NAKASEKO et NISHIMURA) – DOSZT & LY, Pl. 5, Fig. 1

1991 *Muelleritortis cochleata tumidospina* KOZUR – DOSZT & LY, Pl. 4, Fig. 5

1991 *Muelleritortis cochleata hungarica* n. ssp. – DOSZT & LY, p. 344, Pl. 5, Figs. 2, 3

1991 *Plafkerium cochleatum* (NAKASEKO & NISHIMURA, 1979) – BRAGIN, p. 80, Pl. 4, Figs. 10, 12; Pl. 5, Fig. 10, Pl. 10, Fig. 6

1992 *Plafkerium* spp., pars – YEH, p. 61, only the specimens on Pl. 7, Figs. 12, 13; Pl. 9, Fig. 16

1993 *Emiluvia* ? *cochleata* NAKASEKO & NISHIMURA – SASHIDA et al.,p. 93, Figs. 8–5, 6, 8, 15, 16

1994 *Muelleritortis cochleata hungarica* DOSZT & LY – DOSZT & LY, Pl. 3, Fig. 4

1994 *Muelleritortis cochleata* (NAKASEKO & NISHIMURA) – DOSZT & LY, Pl. 3, Fig. 5

Description: With the character of the genus. Cortical shell spherical or subspherical, in polar view circular to quadratic with the corners between the main spines. In the latter type a shallow depression is present in the equatorial plane of the main spines. Outer pore frames very strong, with big, very distinct nodes on the vertices. All main spines are distally pointed and prolonged in a needle-like short spine. The untwisted main spine is distinctly longer than the 3 twisted main spines. The main spines are mostly parallel-sided in their proximal part and taper slowly in their distal part. More rarely, the main spines are distally expanded, before they are tapering. Central furrow of the ridges on the main spine mostly deep and broad, partly strongly reduced and shallow.

Occurrence: Very common in the middle to late Longobardian *Budurovignathus mungoensis* conodont zone. Tethys, Japan, Philippines, British Columbia.

Remarks: Several subspecies can be discriminated. In *M. cochleata cochleata* (NAKASEKO & NISHIMURA, 1979) (Pl. 1, Fig. 9, Pl. 3, Fig. 1) the cortical shell is spherical, its outline in polar view is round, the main spines are distally not or only indistinctly widened.

Muelleritortis cochleata minoensis (NAKASEKO & NISHIMURA, 1979) (Pl. 1, Figs. 6, 10) has the same character of the main spines, but the cortical shell is quadratic in polar view, with the corners between the main spines. A slight depression of the cortical shell is present in the equatorial plane between the main spines. The median groove on at least some main spine ridges is indistinct, but this feature is rather variable in several *Muelleritortis* species and has no taxonomic importance.

In *Muelleritortis cochleata koeveskalensis* KOZUR, 1988 (Pl. 1, Fig. 7; Pl. 2, Figs. 1, 8; Pl. 3, Fig. 3) the twisted main spines are distinctly expanded before the pointed distal end. The outline of the cortical shell in polar view is subquadratic with the corners between the main spines. Between the main spines the shell is slightly depressed in the equatorial plane.

Muelleritortis cochleata tumidospina KOZUR, 1988 is discussed below.

Muelleritortis cf. *cochleata koeveskalensis* KOZUR, 1988
(Pl. 2, Fig. 4)

1990 *Plafkerium* sp. – GORICAN & BUSER, p. 153, Pl. 6, Fig. 9

Remarks: All 4 main spines have the same length. In contrast, in typical *Muelleritortis cochleata koeveskalensis* KOZUR, 1988 (Pl. 1, Fig. 7; Pl. 2, Figs. 1, 8; Pl. 3, Fig. 3), the untwisted main spine is distinctly longer than the twisted ones. The taxonomic importance of this difference is not clear. In all other features M. cochleata koeveskalensis and M. cf. *cochleata koeveskalensis* are identical. Similarly, also in *Muelleritortis* cf. *cochleata cochleata* (NAKASEKO & NISHIMURA, 1979) (Pl. 3, Fig. 1) the untwisted spine has about the same length as the twisted ones. Also this form is in all other fea-

tures identical with typical *M. cochleata cochleata*, in which the untwisted main spine is distinctly longer than the twisted ones. Therefore probably the relative length of the untwisted main spines compared with the twisted main spines is taxonomically not important within *M. cochleata*. However, this feature has to be investigated in stratigraphic sequences. In the slightly older material from the basal *Budurovignathus mungoensis* Zone of Köveskál (Hungary), numerous specimens of *M. cochleata cochleata* occur and in all specimens the untwisted main spine is considerably longer than the twisted ones. In the material from Varoski Creek, however, in most specimens of *M. cochleata cochleata* the untwisted main spine has either about the same length as or it is not very much longer than the twisted main spines.

Muelleritortis cochleata tumidospina KOZUR, 1988

1986 *Emiluvia* (?) aff. *cochleata* NAKASEKO & NISHIMURA – BRAGIN, Pl. 2, Fig. 8
1988 *Muelleritortis cochleata tumidospina* n. subsp. – KOZUR, p. 54, Pl. 3, Fig. 2
1991 *Muelleritortis cochleata tumidospina* KOZUR – DOSZT & LY, Pl. 4, Fig. 5
1991 *Plafkerium cochleatum* (NAKASEKO & NISHIMURA, 1979), pars – BRAGIN, p. 80, Pl. 4, Fig. 10, non! Fig. 12; non! Pl. 5, Fig. 10; non! Pl. 10, Fig. 6
1992 *Plafkerium* spp., pars – YEH, p. 61, only the specimen on Pl. 7, Fig. 13

Occurrence: Middle Longobardian (lower *Budurovignathus mungoensis* conodont zone) of Hungary, Philippines and Russian Far East.

Remarks: The main spines are broader than in *Muelleritortis cochleata cochleata* (NAKASEKO & NISHIMURA, 1979). The pore frames of the outer layer display smaller nodes than in *M. cochleata cochleata*. The pores of the outer layer differ very much in size and shape within one specimen. The outline of the cortical shell in polar view is subcircular to subquadratic with slight extensions in direction of the main spines. By the latter three

features some similarities to the *Muelleritortis quadrata* group can be observed.

Muelleritortis bosniensis n. sp.
(Pl. 2, Figs. 7, 11)

Derivation of name: According to the occurrence in the Republic of Bosnia-Hercegowina.
Holotype: The specimen on Pl. 2, Fig. 11; rep.-no. Komo 1994 III-9
Material: 12 specimens.
Diagnosis: Cortical shell globular, very large, covered in the equatorial region or in most of the cortical shell with a spongy layer. Below this spongy layer the typical two-layered structure is present. The outer of these layers has high pore frames with large roundish pores and nodes on the vertices. The 4 main spines are cross-like arranged. The untwisted main spine is longer to much longer than the twisted ones. All main spines are parallel-sided or insignificantly widened in distal direction. Distal ends of all main spines pointed. Median groove of the ridges on the main spines very broad and deep. On the untwisted main spine the median groove and the furrows between the ridges have about the same width and depth (secondarily hexacarinate).
Measurements:
Diameter of the cortical shell: 160–212 µm
Length of the untwisted main spine: 96–163 µm
Length of the twisted main spines: 60–80 µm
Occurrence: Early late Longobardian of the type locality.
Remarks: By the large globular cortical shell, in which the two layers are partly to nearly totally covered by an spongy layer, *Muelleritortis bosniensis* n. sp. is well distinguished from all other *Muelleritortis* species.

Muelleritortis expansa n. sp.
(Pl. 1, Figs. 1–5, 8?)

? 1983 *Emiluvia* ? *cochleata* NAKASEKO & NISHIMURA – NISHIZONO & MURATA, Pl. 2, Fig. 7

Derivatio nominis: According to the widened distal part of the main spines.
Holotype: The specimen on Pl. 1, Fig. 2; rep.-no. KOMO 1994 III-2
Material: More than 100 specimens.
Diagnosis: With the character of the genus. Cortical shell in polar view quadratic to subquadratic with the corners in direction of the main spines. Outer pore frames moderately high, with irregular large and small pores. Nodes on the vertices absent or very small. The 4 very broad main spines are arranged cross-like and have all the same length. The 3 twisted main spines are distally expanded, their distal ends are round, blunt, rarely rounded pointed, without terminal spine. The untwisted main spine is distally slightly expanded, rarely parallel-sided. Its distal end is round to rounded pointed. A rather strong and long terminal spine is always present. The ridges of all 4 main spines display a very broad and deep median groove producing secondarily hexacarinate character of the main spines.
Measurements
Diameter of cortical shell: 117–133 µm
Length of main spines: 100–133 µm
Occurrence: Middle to late Longobardian of the Tethys and Japan.
Remarks: In *Muelleritortis cochleata* (NAKASEKO & NISHIMURA, 1979) the untwisted main spine is in general distinctly longer than the twisted ones. The shell is either circular to subcircular in polar view or, if it is quadratic in polar view, the corners are situated between the main spines and not in their direction.

The twisted main spines of *Muelleritortis quadrata* n. sp. are distally not or only a little widened. The pore frames of the outer layer of the cortical shell are lower, often indistinct, in the equatorial part mostly missing.

Muelleritortis quadrata n. sp.
(Pl. 2, Figs. 2, 5; Pl. 3; Figs. 2, 6)

Derivation of name: According to the quadratic outline of the cortical shell in polar view.

Holotype: The specimen on Pl. 2, figs. 2; rep.-no. KOMO 1994 III-5

Diagnosis: With the character of the genus. Cortical shell with quadratic outline in polar view, corners in direction of the main spines. Pore frame of outer layer often indistinct, rarely absent, in the equatorial part always very low or absent. No nodes on the vertices. Pores of the outer layer very irregular in size and shape. The 4 main spines are moderately broad, all about of the same length. They are distally slightly widened, but display a pointed distal end, in the untwisted main spine a tiny terminal spine may be present. The median groove of the 3 ridges of the main spine is deep and broad.

Measurements: See under the subspecies.

Occurrence: Common in the early late Longobardian at the type locality.

Remarks: By the low, often indistinct, rarely even absent outer layer, this species is well distinguished from other *Muelleritortis* species.

Muelleritortis expansa n. sp. is additionally distinguished by broader main spines that have a distinct distal widening at least in the twisted main spines, but often also the untwisted one. The twisted main spines display a round, blunt, rarely rounded pointed distal end. The untwisted main spine ends in a large terminal spine.

In *Muelleritortis* cf. *quadrata* the cortical shell has a subquadratic outline in polar view. The pore frames of the outer layer are unreduced, in the polar part moderately high, in the equatorial region lower, but also distinct.

According to distinct difference in the length of the main spines two subspecies can be discriminated which are described below.

Muelleritortis quadrata quadrata n. subsp.
(Pl. 2, Fig. 2; Pl. 3, Fig. 6)

Derivation of name and holotype: See species.

Diagnosis: With the character of the species. Main spines relatively long. The torsion of the 3 twisted main spines is rather weak. Pore frames of the outer layer very low and indistinct, present only in the polar region. In few specimens the other layer is totally absent.

Measurements:
Diameter of cortical shell (measured between the parallel sides): 160–173 µm
Length of the main spines: 150–160 µm

Occurrence: As for the species.

Remarks: *Muelleritortis quadrata parvispina* n. subsp. displays shorter main spines, the pores frames of the outer layer are in the polar region always distinct and only in the equatorial region indistinct or missing.

Muelleritortis ? *firma* (GORIČAN in GORIČAN & BUSER, 1990) displays four untwisted main spines or three spines may be very little twisted. The cortical shell has a subquadratic outline in polar view and the pore frames of the outer layer are high with distinct nodes on the vertices.

Muelleritortis quadrata parvispina n. subsp.
(Pl. 2, Fig. 5; Pl. 3, Fig. 2)

Derivation of name: According to the short main spines.

Holotype: The specimen on Pl. 3, Fig. 2; rep.-no. KOMO 1994 III-8

Diagnosis: With the character of the species. Pore frames of the outer layer in the polar region of the cortical shell distinct, in the equatorial region either indistinct or missing.

Measurements:
Diameter of cortical shell (measured between the parallel sides): 172–180 µm
Length of main spines: 93–127 µm

Remarks: *Muelleritortis quadrata quadrata* n. subsp. has longer main spines and the pore frames of the outer layer on the cortical shell are in general very low and often indistinct.

Muelleritortis pulchra rotunda n. subsp.
(Pl. 1, Fig. 11)

Derivation of name: According to rounded distal end of the twisted main spines.

Holotype: The specimen on Pl. 1, Fig. 11; rep.-no. Komo 1994 III-4

Material: 4 specimens.

Diagnosis: With the character of the genus. Cortical shell subglobular with subcircular outline in polar view. Pore frames of the outer layer low to moderately high, with large, irregular pores. Nodes on the vertices absent or small. The 4 main spines are not cross-like arranged. The twisted main spine opposite to the untwisted one is situated somewhat oblique to the axis of the untwisted main spine. The other two twisted main spines are situated at an angle of about 60° to the third untwisted main spine. The untwisted main spine is considerably longer than the 3 twisted ones, nearly parallel-sided with pointed posterior end. Median groove of the ridges on the main spines deep and very broad (secondarily hexacarinate main spines).

Measurements:

Diameter of cortical shell: 116–130 µm

Length of the untwisted main spine: 126–137 µm

Length of the twisted main spines: 79–106 µm

Occurrence: Early late Longobardian at the type locality.

Remarks: In *Muelleritortis pulchra pulchra* Kozur, 1988 the pore frames of the outer layer are very high with big nodes on the vertices. The size difference between the untwisted main spine and the twisted ones is larger, the twisted main spines have a pointed distal end and they are situated near each other around the opposite side of the untwisted main spine.

In all other *Muelleritortis* species the 4 main spines are cross-like arranged.

Muelleritortis sp.
(Pl. 2, Fig. 6)

Remarks: Only one specimen of a *Muelleritortis* with large globular shell and relatively short, broad main spines is present. The pore frames are very high, with round nodes on the vertices. In the equatorial area the pore frames are somewhat lower, but also high. One of the twisted main spi-

nes lies perpendicularly to the polar axis, the other one lies obliquely to this axis.

Genus *Pentatortis* Kozur, 1988

Type species: *Pentatortis longobardica* Kozur, 1988

Pentatortis longobardica Kozur, 1988
(Pl. 2, Fig. 10)

Occurrence: Miuddle Longobardian to early late Longobardian of Hungary and Bosnia-Hercegowina.

Remarks: *Pentatortis longobardica* Kozur, 1988 is characterized by three twisted main spines in a plane perpendicular or oblique to the axis of the untwisted main spine. The fourth twisted main spine lies either opposite to the untwisted main spine or somewhat oblique to its axis. The derivation of this species from *Muelleritortis* with 4 cross-like arranged main spines is rather clear. In *Muelleritortis* one twisted main spine lies either opposite to the untwisted main spine or somewhat oblique to its axis. The two other twisted main spines are situated in a plane perpendicular or somewhat oblique to the axis of the untwisted main spine. In *Pentatortis longobardica* an additional twisted main spine lies in latter plane. The arrangement of the main spines in *Pentatortis krystyni* n. sp. is different (see below).

Pentatortis krystyni n. sp.
(Pl. 2, Fig. 9)

Derivation of name: In honour of Prof. L. Krystyn, Vienna.

Holotype: The specimen on Pl. 2, Fig. 9; rep.-no. Komo 1994 III-10

Material: 7 specimens.

Diagnosis: Cortical shell globular. Outer pore

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frames high with roundish, mostly large pores, at the base of the main spines somewhat elongated in their directions. Vertices of the pore frames with nodes. The 5 main spines are broad, in distal direction a little widened, with pointed or roundish pointed distal end. They are about of the same length or the untwisted main spine is a little longer than the twisted ones. Median groove of the main spines wide and deep. Especially the untwisted main spine is secondary hexacarinate. The untwisted main spine and two of the twisted ones are situated in triangular arrangement in one plane. Two further twisted main spines are present in some distance of one of the twisted main spines.

Measurements:
Diameter of the cortical shell: 176–200 µm
Length of the untwisted main spine: 133–140 µm
Length of the twisted main spines: 112–133 µm
Occurrence: In the early late Longobardian at the type locality.
Remarks: *Pentatortis longobardica* KOZUR, 1988 is distinguished by the arrangements of the main spines (see above).

Pentatortis hexaspina n. sp.
(Pl. 3, Figs. 4, 5)

Derivation of name: According to the presence of 6 main spines.
Holotype: The specimen on Pl. 3, Fig. 4; rep.-no. KOMO 1994 III-11
Material: 5 specimens.
Diagnosis: Cortical shell globular to subglobular. Pore frames of the outer layer high, with nodes on the vertices. Pores of the outer layer differ in size and shape, most of them are large, roundish, at the base of the main spines elongated. The 6 main spines are parallel-sided or very little widened in distal direction. The untwisted main spine is longer than the twisted ones. The distal end of the untwisted main spine is pointed, the distal end of the twisted main spines is rounded, but often with a tiny terminal spine. Median groove of the main spine ridges broad and deep (secondarily hexacarinate main spines). One of the twisted main spines

lies opposite to the untwisted main spine, but mostly somewhat oblique to its axis (subpolar arrangement with respect to the untwisted main spine). Three of the twisted main spines are situated in a plane, perpendicularly or somewhat oblique to the axis of the untwisted main spine. A fifth twisted main spine lies between this plane and the subpolar twisted main spine.
Measurements:
Diameter of cortical shell: 122–150 µm
Length of the untwisted main spine: 125–167 µm
Length of the twisted main spines: 65–94 µm
Occurrence: Early late Longobardian at the type locality.
Remarks: In *Pentatortis longobardica* KOZUR, 1988 only 4 twisted main spines are present situated opposite to the untwisted main spine and in a plane perpendicularly or somewhat oblique to the axis of the untwisted main spine.

Genus *Tritortis* KOZUR, 1988

Type species: *Sarla ? kretaensis* KOZUR & KRAHL, 1984

Tritortis kretaensis dispiralis (BRAGIN, 1986)
(Pl. 3, Fig. 11)

1986 *Sarla dispiralis* sp. nov – BRAGIN, p. 67, Fig. 12
1988 *Tritortis kretaensis subcylindrica* n. subsp. – KOZUR, p. 98–99, Pl. 4, Figs. 6, 8
1991 *Sarla dispiralis* BRAGIN, 1986, pars – BRAGIN, p. 79, Pl. 4, Fig. 11; Pl. 5, Fig. 8; non Pl. 4, Fig. 6
1991 *Sarla kretaensis robusta* n. ssp. - DOSZT & LY, p. 197, Pl. 1, Figs. 1, 2
Description: Cortical shell subglobular, in polar view with subcircular, subtriangular or triangular outline. Inner layer with small roundish pores, outer layer with high pore frames and large polygonal or roundish pores and nodes on the vertices. The 3 main spines have about the same length or the untwisted main spine is somewhat longer than

the twisted one. The sides of the main spines are parallel or there is an insignificant distal widening. The distal ends are rounded, blunt or shortly pointed, with short terminal spine. The median groove on the main spine ridges is deep and wide (secondary hexacarinate main spines).

Occurrence: Upper part of middle Longobardian to early Cordevolian of the Tethys.

Remarks: KOZUR (1988 a, b) discriminated two species within *Tritortis*, the middle Longobardian *Tritortis balatonica* KOZUR, 1988 and *Tritortis kretaensis* (KOZUR & KRAHL, 1984). The latter species was subdivided into two subspecies, *T. kretaensis kretaensis* and *T. kretaensis subcylindrica* KOZUR, 1988. *T. kretaensis kretaensis* appeared in the late Longobardian and it is the dominating form and radiolarian index species of the early Cordevolian. *T. kretaensis subcylindrica* occurs in the middle Longobardian and early Cordevolian. It is a transitional form between *T. balatonica* and *T. kretaensis*.

BRAGIN (1986, 1991) described *Sarla dispiralis* BRAGIN, 1986. He assigned to this species forms that correspond both to *T. kretaensis kretaensis* and to *T. kretaensis subcylindrica*. Therefore *Sarla dispiralis* exactly corresponds to *Tritortis kretaensis* by KOZUR (1988). The holotype of *Sarla dispiralis* corresponds to *T. kretaensis subcylindrica*. Therefore *Sarla dispiralis* BRAGIN, 1986 is a junior synonym of *Tritortis kretaensis* (KOZUR & KRAHL, 1984), whereas *T. kretaensis subcylindrica* KOZUR, 1988 is a junior synonym of *Tritortis kretaensis dispiralis* (BRAGIN, 1986). *Sarla kretaensis robusta* DOSZT & LY, 1991 is a further junior synonym of *Tritortis kretaensis dispiralis* BRAGIN, 1986.

Tritortis kretaensis kretaensis (KOZUR & KRAHL, 1984) displays in general more slender main spines that taper slowly and gradual toward the very pointed distal end. The morphological differences between both subspecies are rather gradual, but their discrimination is supported by different stratigraphic ranges. *T. kretaensis kretaensis* begins only in the late Longobardian, whereas *T. kretaensis dispiralis* begins in the upper part of the middle Longobardian. In the Cordevolian *T. kretaensis kretaensis* clearly domi-

nates over *T. kretaensis dispiralis*. The Late Anisian-Early Ladinian age of *T. kretaensis kretaensis* established by CORDEY et al. (1988) for specimens from British Columbia cannot be confirmed. The accompanying *Spongoserrula* is in the Tethys restricted to the middle Longobardian to Cordevolian.

Whereas *T. kretaensis dispiralis* is so far only known from the Tethys, *T. kretaensis kretaensis* is common also in the Circum-Pacific realm (Philippines, Japan., British Columbia).

Tritortis balatonica KOZUR 1988 from the lower part of middle Longobardian displays a globular cortical shell.

Tritortis latispina n. sp.
(Pl. 3, Figs. 7, 8)

Derivation of name: According to the very broad main spines.

Holotype: The specimen on Pl. 3, Fig. 8; rep.-no. KOMO 1994 III-13

Material: 21 specimens.

Diagnosis: Cortical shell subglobular, in polar view with subcircular to subtriangular outline. Outer layer with high pore frames and large polygonal pores of different shape and size. Vertices with small nodes. The three main spines in triangular arrangement are very broad, mostly slightly widened in distal direction. Their distal ends are rounded or blunt, in the untwisted main spine with a distinct terminal spine. The untwisted main spine has about the same length as the twisted ones or it is a little longer. Median groove on the ridges deep, moderately wide.

Measurements:

Diameter of cortical shell: 109–140 µm

Length of the main spines (without terminal spines): 90–119 µm

Maximum width of the main spines: 65–100 µm

Occurrence: Early late Longobardian at the type locality.

Remarks: Most similar are the contemporaneous, stratigraphically oldest representatives of *Tritortis kretaensis dispiralis* (BRAGIN, 1986) which have

rather broad main spines, but not as broad as in *T. latispina* n. sp. Moreover, the terminal spine of the untwisted main spine is very small or absent in *T. kretaensis dispiralis*. Late Longobardian and Cordevolian representatives of *T. kretaensis* display by far narrower main spines.

In *Tritortis acutangulata* n. sp., which has the same form of the main spines, the two twisted main spines are situated near to each other on the opposite side of the untwisted main spine.

Tritortis acutangulata n. sp.
(Pl. 3, Figs. 9, 10)

Derivation of name: According to the arrangement of the twisted main spines at an acute angle.
Holotype: The specimen on Pl. 3, Fig. 10; rep.-no. KOMO 1994 III-15
Material: 5 specimens.
Diagnosis: Cortical shell subglobular, often a little elongated in prolongation of the untwisted main spine. Pore frames of the outer layer high, with large, polygonal pores of different shape, near the base of the main spines elongated. Vertices with small nodes. All three main spines are very broad, subcylindrical with insignificant widening in distal direction. The two twisted main spines are situated in subpolar position to the untwisted main spine. They lie near to each other at an acute angle. Distal ends of the main spines blunt or broadly rounded, in the untwisted main spine with moderately large terminal spine. The untwisted main spine is longer than the two twisted ones. Median groove on the main spine ridges deep and wide. On the untwisted main spine secondary, narrow, a short median groove is present on the wedges of the divided ridges. By this, the untwisted main spine is hexacarinate with ridges divided by a secondary median groove.
Measurements:
Diameter of cortical shell: 120–132 µm
Length of the untwisted main spine (without terminal spine): 125–146 µm
Length of the twisted main spines: 80–123
Maximum width of the main spines: 70–85 µm

Occurrence: Early late Longobardian at the type locality.

Remarks: By the arrangement of the two twisted main spines near to each other at an acute angle, this species can be easily distinguished from all other *Tritortis* species. Most similar is *Tritortis latispina* in which, however, the very broad main spines are arranged in triangular position, like in all other *Tritortis* species. *Tritortis acutangulata* may be a transitional form from *Tritortis latispina* to *Ditortis* that has two main spines (a twisted and an untwisted one) in bipolar position. In specimens of *T. acutangulata*, in which the two twisted main spines are very near to each other, the arrangement of the main spines is nearly bipolar.

Tritortis inaequispina n. sp.
(Pl. 3, Fig. 12)

Derivation of name: According to the strongly different size of the main spines.
Holotype: The specimen on Pl. 3, Fig. 12; rep.-no. KOMO 1994 III-17
Material: 2 specimens.
Diagnosis: Cortical shell globular. Outer pore frames high, with small nodes on the vertices and large polygonal or roundish polygonal pores of different shape and size. Untwisted main spine large, broad, pointed, with moderately long terminal spine. Twisted spines much smaller, short, narrow, rapidly tapering towards the pointed distal end. One twisted main spine is situated opposite to the untwisted main spine, the other one about perpendicular to it. The ridges on the untwisted main spine are subdivided by a deep, moderately broad median groove. On the twisted main spine only in the basal part an indistinct shallow median groove is present on the ridges.
Measurements:
Diameter of cortical shell: 110–120 µm
Length of the untwisted main spine (without terminal spine): 108–112 µm
Maximum width of the untwisted main spine: 60–64 µm
Length of the twisted main spines: 70–75 µm

Maximum width of the twisted main spines: 25–31 μm

Occurrence: Very rare in the early late Longobardian at the type locality.

Remarks: This species seems to be a transitional form between *Tritortis* and *Ditortis*. The untwisted main spine and one of the twisted main spines are in bipolar position, like in *Ditortis*, but because of the presence of the second twisted main spine, this species is assigned to *Tritortis*.

3. Biostratigraphic evaluation

The Muelleritortiidae are dominant and easily determinable radiolarians of the Tethyan Longobardian and Cordevolian. In the Early Longobardian *Budurovignathus hungaricus* Zone Muelleritortiidae with one untwisted main spine and one to five twisted main spines are missing. There occur only forms without twisted main spines (*Muelleritortis ? firma* group), which may be the forerunners of *Muelleritortis cochleata*. At the base of the middle Longobardian (base of the *Budurovignathus mungoensis* conodont zone), *Muelleritortis cochleata* has its first appearance. This species dominates the entire middle and late Longobardian Muelleritortiid faunas. In the middle Longobardian, *Tritortis* is very rare, in the lower part represented by *Tritortis balatonica*, in the upper part by primitive *Tritortis kretaensis dispiralis*. Typical *Tritortis kretaensis kretaensis* began only immediately below the Ladinian-Carnian boundary. A little later, at the base of the Cordevolian, defined by the first appearance of the conodonts *Budurovignathus diebeli* (KOZUR & MOSTLER) and *Paragondolella polygnathiformis* (BUDUROV & STEFANOV), *Muelleritortis* becomes suddenly very rare and these faunas are dominated by *Tritortis kretaensis kretaensis*, the index species of the early Cordevolian *T. kretaensis* Zone.

Pentatortis with 3 species was so far only found in the middle and early late Longobardian, but this genus is rather rare. The likewise rare *Ditortis* was so far only found in the late Longobardian.

Muelleritortis cochleata and the *Tritortis kretaensis* lineage are very important for stratigraphic subdivisions. Radiolarian faunas, in which *Muelleritortis cochleata* dominates the Muelleritortiidae, belong to the middle and late Longobardian *Muelleritortis cochleata* Zone which perfectly coincides with the *Budurovignathus mungoensis* conodont zone. If *Tritortis kretaensis* dominates the Muelleritortiidae, the faunas belong to the early Cordevolian *Tritortis kretaensis* Zone. The change from a *Muelleritortis cochleata* dominated into a *Tritortis kretaensis kretaensis* dominated fauna occurs in the Dallapuszta section of Darnó-hegy (Hungary) within a very short interval of a few cemtinmetres of red radiolarites. In the upper part of the *M. cochleata* Zone, *Tritortis kretaensis dispiralis* is common.

Muelleritortis cochleata and *Tritortis kretaensis* are common in the Tethys and in the Circum-Pacific realm (Japan, Philippines, British Columbia). Other stratigraphically important Longobardian and Cordevolian forms, like advanced Oertlispongidae, are outside the Tethys missing or rare.

CORDEY et al. (1988) placed a radiolarian fauna with *Muelleritortis cochleata*, *Tritortis kretaensis kretaensis*, *Spongoserrula dosztalyi n. sp.* (= *Spongoserrula rarauana* DUMITRICĂ sensu CORDEY et al., 1988) and *Spongoserrula dehli* CORDEY et al. into the Late Anisian to Early Ladinian on the base of "*Gondolella*" *constricta* MOSHER & CLARK. However, in North America many different forms have placed into *Neogondolella constricta* and therefore this species give not too much age evidences. On the other side, in radiolarian faunas with *Tritortis kretaensis* from the Tethys, conodonts similar to *N. constricta* are absent. Unfortunately, no data are given about the relative frequency of *M. cochleata* and *T. kretaensis*. Because all figured *Tritortis kretaensis* belong to *T. kretaensis kretaensis*, the age of this radiolarian fauna is either late Longobardian or early Cordevolian. A late Longobardian to Cordevolian age is also indicated by the two *Spongoserrula* species with pointed to needle-like spines that begin only in the upper subzone (*Spongoserrula fluegeli* Subzone) of the *Muelleritortis cochleata* Zone. In the Tethys, the genus *Spongoserrula* does not occur

before the Longobardian *Budurovignathus mungoensis* conodont zone. A late Anisian to early Ladinian age can be therefore excluded, even if we have to take into consideration the stratigraphically higher position of the Anisian-Ladinian boundary in North America compared with the priority boundary at the base of the *Reitziites reitzi* Zone. *Spongoserrula*-bearing beds belong also according the North American standard to the Longobardian.

Our investigated material belongs to the lower part of the *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (lower part of upper *cochleata* Zone). *Tritortis balatonica*, present in the lower part of this zone, is already replaced by *T. kretaensis dispiralis* which occurs from the middle part of the *M. cochleata* Zone up to the early Cordevolian. On the other hand, *T. kretaensis kretaensis* which begins in the late Longobardian is not yet present.

The detailed subdivision of the *Muelleritortis cochleata* Zone is based on the development of advanced Oertlispongidae and will be discussed in KOZUR & MOSTLER (in press). The lower subzone (*Pterospongus alatus* Subzone) of the *M. cochleata* Zone is characterized by advanced *Falcispongus*, advanced *Baumgartneria*, very primitive *Scutispongus* of the *S. rostratus* group, and above al several *Pterospongus* species. The last *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER, an important Fassanian guideform, is still present. Denticulated *Spongoserrula species* are absent.

The middle subzone (*Spongoserrula rarauana* Subzone) of the *M. cochleata* Zone is characterized by primitive *Spongoserrula* with rounded spines (*S. rarauana* group). The guideforms of the *Pterospongus alatus* Subzone are still present in decreasing frequency.

The upper subzone (*Spongoserrula fluegeli* Subzone) of the *M. cochleata* Zone is characterized by advanced *Spongoserrula* with pointed or needle-like spines (*S. fluegeli* group) and *Steigerispongus* with pointed spines. In the lower part of this subzone *Spongoserrula* of the *S. rarauana* group are still present, in the upper subzone they become very rare or are absent.

In the early Cordevolian advanced Oertlispongidae are still common (dominated by advanced *Spongoserrula* of the *S. fluegeli* group). In the late Cordevolian Oertlispongidae are very rare. Except advanced *Spongoserrula* of the *S. fluegeli* group, few *Scutispongus* and *Bogdanella* are present.

The Muelleritortiidae are better suitable for the discrimination of zones (middle and late Longobardian *M. cochleata* Zone and Cordevolian *Tritortis kretaensis* Zone) than the Oertlispongidae, because Muelleritortiidae are worldwide common forms. However, in the Tethyan Triassic, the Oertlispongiidae are most important for definition of subzones, because they underwent the most rapid morphlogic changes during the Ladinian time. Unfortunately, outside the Tethyan realm, Oertlispongidae are rare.

Acknowledgements

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Authors' addresses:
Dr. sc. Heinz Kozur, Rézsü u. 83, H-1029 Budapest, Hungary; Univ.-Prof. Dr. Helfried Mostler, Institute of Geology and Paleontology, University of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria.

Explanation of Plates

All figured radiolarians are from a micritic limestone of the locality Varoski Creek near Fojnica, south of Sarajevo (Republic Bosnia-Hercegowina). They belong to the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian).

Plate 1

Plate 2

Figs. 1, 8: *Muelleritortis cochleata koeveskalensis* KOZUR, 1988, fig. 1: x 180, rep.-no. KOMO 1994 III-23, Fig. 8: x 170, rep.-no. KOMO 1994 III-24

Fig. 2:   *Muelleritortis quadrata quadrata* n. subsp., holotype, x 150, rep.-no. KOMO 1994 III-5.

Fig. 3:   *Muelleritortis* cf. *quadrata* n. sp., x 160, rep.-no. KOMO 1994 III-6.

Fig. 4:   *Muelleritortis* cf. *cochleata koveskalensis* KOZUR, 1988, x 160, rep.-no. KOMO 1994 III-1.

Fig. 5:   *Muelleritortis quadrata parvispina* n. subsp., x 150, rep.-no. KOMO 1994 III-7.

Fig. 6:   *Muelleritortis* sp., x 170, rep.-no. KOMO 1994 III-25.

Figs. 7, 11: *Muelleritortis bosniensis* n. sp.; Fig. 7. paratype, x 160, rep.-no. KOMO 1994 III-26; Fig. 11: holotype, x 250, rep.-no. KOMO 1994 III-9.

Fig. 9:   *Pentatortis krystyni* n. sp., holotype, x 150, rep.-no. KOMO 1994 III-10.

Fig. 10:   *Pentatortis longobardica* KOZUR, 1988, x 180, rep.-no. KOMO 1994 III-27.
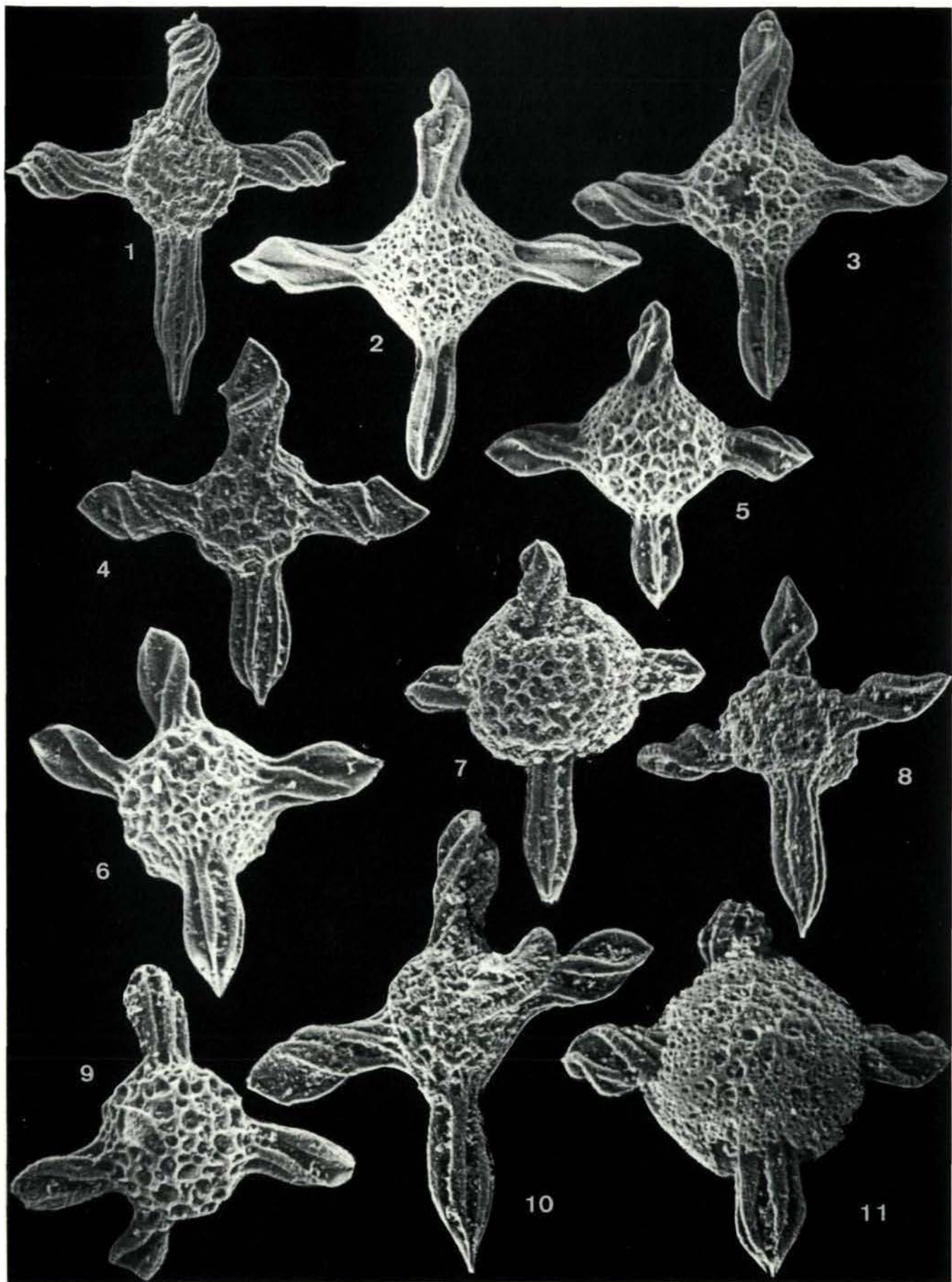
Plate 3

Fig. 1.   *Muelleritortis* cf. *cochleata cochleata* (NAKASEKO & NISHIMURA, 1979), x 150, rep.-no. KOMO 1994 III-28.

Fig. 2:   *Muelleritortis quadrata parvispina* n. subsp., holotype, x 150, rep.-no. KOMO 1994 III-8.

Fig. 3:   *Muelleritortis cochleata koeveskalensis* KOZUR, 1988, x 160, rep.-no. KOMO 1994 III-29.

Figs. 4, 5: *Pentatortis hexaspina* n. sp.; Fig. 4: holotype, x 200, rep.-no. KOMO 1994 III-11; Fig. 5: x 180, rep.-no. KOMO
            1994 III-30.

Fig. 6:   *Muelleritortis quadrata quadrata* n. subsp., x 150, rep.-no. KOMO 1994 III-31.

Figs. 7, 8: *Tritortis latispina* n. sp., Fig. 7: x 200, rep.-no. KOMO 1994 III-14, fig. 8: holotype, x 210, rep.-no. KOMO 1994 III-
            13.

Figs. 9, 10: *Tritortis acutangulata* n. sp.; Fig. 9: x 200, rep.-no. KOMO 1994 III-16; fig. 10: holotype, x 130, rep.-no. KOMO 1994
            III-15.

Fig. 11:   *Tritortis kretaensis dispiralis* (BRAGIN, 1986), primitive specimen, x 190, rep.-no. KOMO 1994 III-12.

Fig. 12:   *Tritortis inaequispina* n. sp., holotype, x 200, rep.-no. KOMO 1994 III-17.
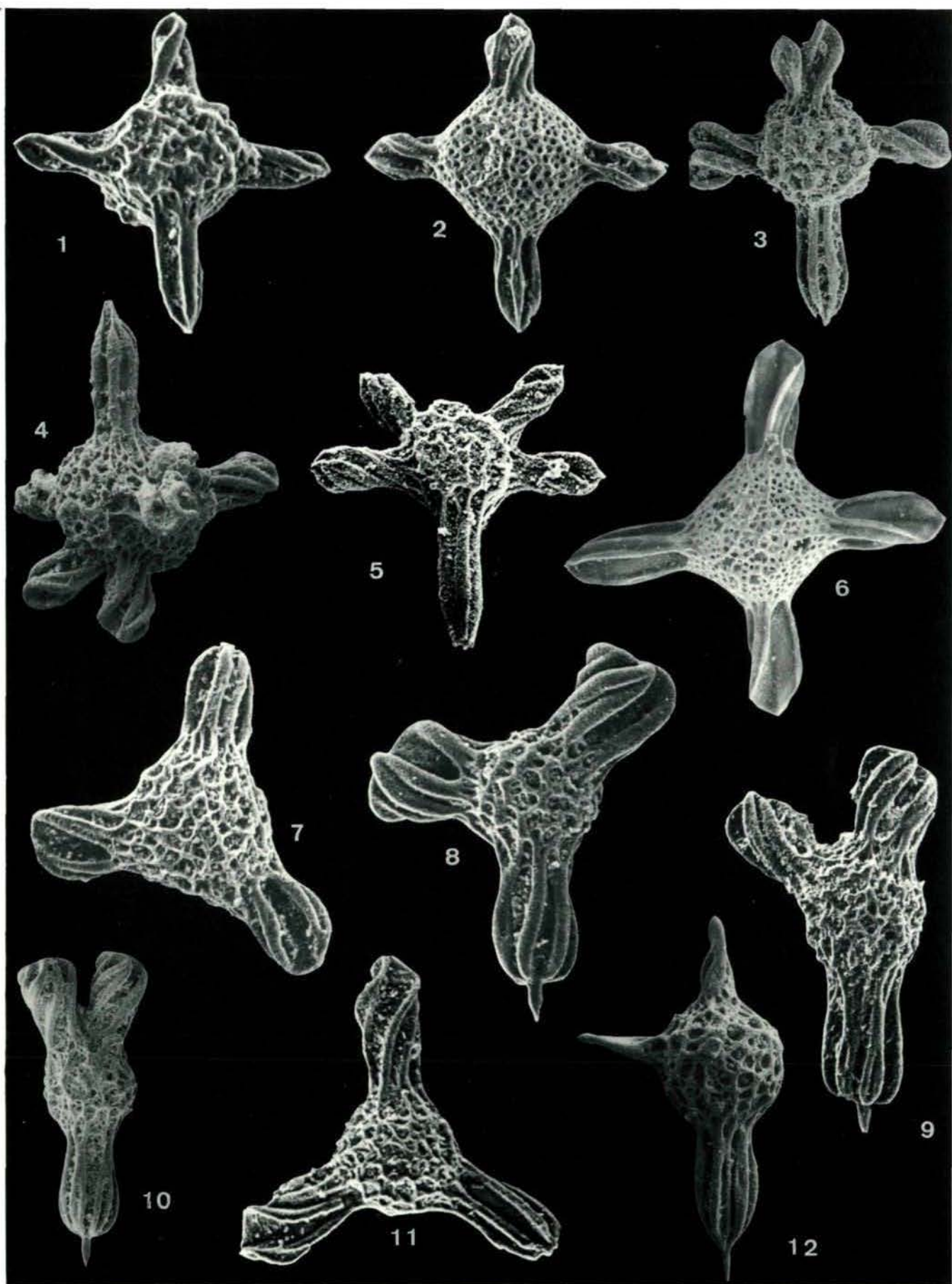
LONGOBARDIAN (LATE LADINIAN) OERTLISPONGIDAE (RADIOLARIA) FROM THE REPUBLIC OF BOSNIA-HERCEGOVINA AND THE STRATIGRAPHIC VALUE OF ADVANCED OERTLISPONGIDAE

Heinz Kozur & Helfried Mostler

With 2 figures, 1 table and 15 plates

Herrn O. Univ.-Prof. Dr. Helmut Flügel zum 70. Geburtstag gewidmet

Abstract:

A very rich radiolarian fauna was found in a limestone with the conodont *Budurovignathus mungoensis* (DIEBEL) at the locality Varoški creek, 2 km W of Fojnica (south of Sarajevo, Republic of Bosnia-Hercegovina). This radiolarian fauna is characteristic of the lower part of the upper subzone (*Spongoserrula fluegeli* Subzone) of *Muelleritortis cochleata* Zone and indicates an early late Longobardian age. The stratigraphically important Oertlispongidae of this fauna are described in the present paper. For comparison, some Oertlispongidae are described from the lower and middle Subzone of the M. cochleata Zone of Southern Alps and from the Cordevolian of Sicily. 84 oertlispongid species and subspecies, 69 of which are new, have been found in the *Muelleritortis cochleata*- and *Tritortis kretaensis* zones (middle Longobardian to Cordevolian) of the Tethys.

Zusammenfassung:

Eine sehr reiche Radiolarienfauna wurde aus einem Kalkstein mit der Conodontenart *Budurovignathus mungoensis* (DIEBEL) von der Lokalität Varoški-Bach, 2 km westlich von Fojnica (südlich von Sarajevo, Republik Bosnien-Herzegowina) nachgewiesen. Diese Radiolarienfauna ist charakteristisch für den unteren Teil der oberen Subzone (*Spongoserrula fluegeli* Subzone) der *Muelleritortis cochleata*-Zone und zeigt frühes-spätlongobardisches Alter an. In der vorliegenden Arbeit werden die stratigraphisch wichtigen Oertlispongidae aus dieser Fauna beschrieben. Zu Vergleichszwecken werden auch einige Oertlispongidae aus der unteren und mittleren Subzone der *M. cochleata*-Zone aus den Südalpen sowie aus dem höheren Cordevol von Sizilien beschrieben. 84 Arten und Unterarten der Oertlispongidae, von denen 69 neu sind, wurden in der *Muelleritortis cochleata*- und *Tritortis kretaensis*-Zone (Mittellongobard-Cordevol) der Tethys nachgewiesen.

1. Introduction

Oertlispongidae KOZUR & MOSTLER (in DUMITRICA et al., 1980) are stratigraphically decisive important radiolarians for the Ladinian of the Tethyan realm. They are characterized by a highly differentiated recurved main (apical) polar spine. Often the end of this polar spine is bifurcated and both ends are recurved. One or both ends of the recurved polar spine may join the shell. On different ways a ring-like structure evolved from the highly differentiated polar spine and by this the saturnalid radiolarians evolved at the base of the Late Triassic from oertlispongid ancestors (KOZUR & MOSTLER, 1983).

The degree of bending, the length of the straight lower part of the main polar spine show taxonomically important differentiations in advanced Oertlispongidae, but also the width of the main polar spine is taxonomically very important. It may become blade-like and sculptured with spines or rounded appendages. The form and sculpture of
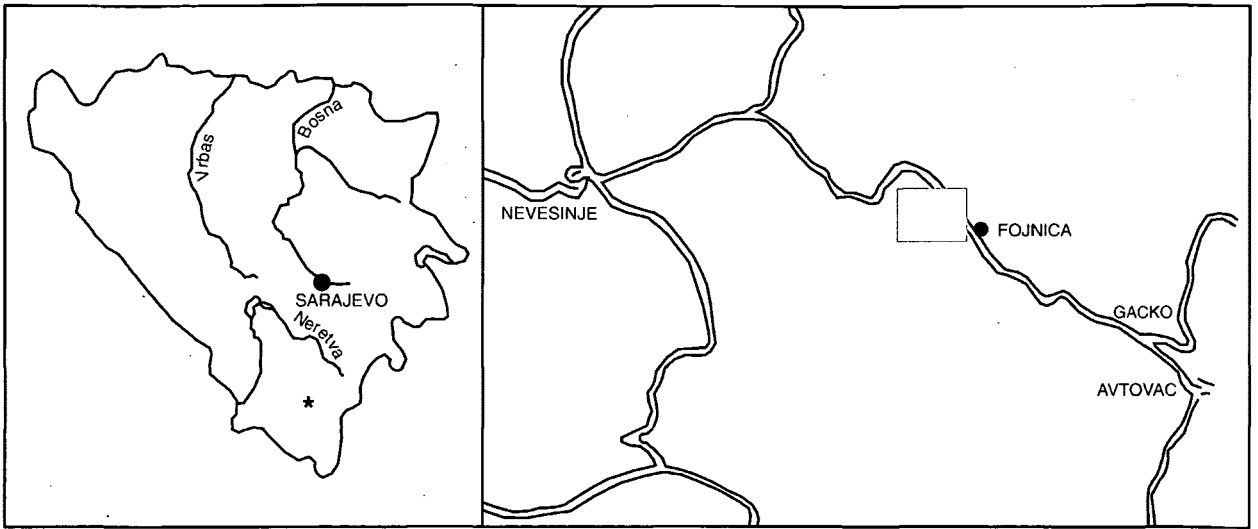
Fig. 1: Locality map. a) Geographic position of the locality (asterisk) in the Republic Bosnia-Hercegowina. b) Detailed locality map from MUDRENOVIĆ & GAKOVIĆ (1964).
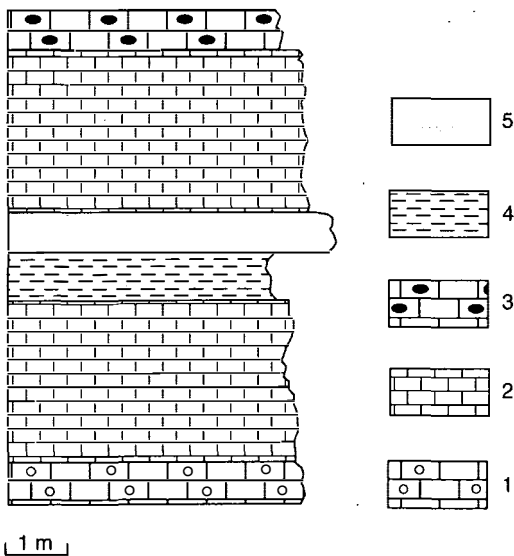
Fig. 2: Lithostratigraphic sequence with radiolarian-bearing limestone below and above a thin radiolarite-tuffit intercalation (from MUDRENOVIĆ & GAKOVIĆ, 1964). Vertical scale indicated.

1 = Calcarenite
2 = radiolarian-bearing limestone
3 = cherty limestone with *Joannites klipsteini* and *J. cymbiformis*
4 = tuffitic claystones
5 = red radiolarite

the main polar spine is so characteristic that genera and species of Oertlispongidae can be easily determined on the base of isolated main polar spines. Several species and genera established by DUMITRICĂ (1982) were based on such isolated main polar spines.

After the Oertlispongidae have been established by KOZUR & MOSTLER (in DUMITRICĂ et al., 1980), this family became one of the stratigraphically most important Triassic radiolarian groups. Advanced Oertlispongidae with differentiated main polar spine characterize the Tethyan Ladinian. Outside the Tethys, Oertlispongidae have been reported from the Philippines (YEH, 1990, 1992), Japan (SASHIDA et al., 1993) and from British Columbia, Canada (CORDEY et al., 1988), but the most Oertlispongidae have been described from the Eurasiatic Tethys (DUMITRICĂ, KOZUR & MOSTLER, 1980, DUMITRICĂ, 1982, DUMITRICĂ & MELLO, 1982, KOZUR & MOSTLER, 1981, 1983, 1994, DE WEVER, 1984, LAHM, 1984, KOLAR-JUR-KOVŠEK, 1989, MARTINI et al., 1989, BUDAI & DOSZTÁLY, 1990, DE WEVER et al., 1990, GORIČAN

& BUSER, 1990, DOSZTÁLY, 1991, 1994, DOSZTÁLY & JÓZSA, 1993). The Oertlispongidae are typical radiolarians of the tropical sea.

As shown by DUMITRICĂ (1982), DOSZTÁLY (1994) and KOZUR & MOSTLER (1994), the Oertlispongidae are extraordinarily important for the Ladinian stratigraphy, both for the definition of the priority Anisian-Ladinian boundary at the base of the *Reitziites reitzi* ammonoid zone and for subdivisions within the Ladinian. Advanced Oertlispongidae are present also in the Cordevolian, but the reports about the occurrence of advanced Oertlispongidae in the Tuvalian by DUMITRICĂ (1982) could not be confirmed. Therefore alone the presence of the easily recognizable isolated recurved main spines of advanced Oertlispongidae can be used as one of the best evidences for Ladinian age, if Cordevolian age can be excluded. This is in so far especially important, because the radiolarian biostratigraphy can be also applied to the widespread radiolarite facies of ancient oceans which is free of any macrofossils and often very poor in conodonts. The stratigraphically important adult platform conodonts are very rare or absent in this facies.

The first Oertlispongidae with recurved main polar spine appeared at the priority base of the Ladinian, at the base of the *Reitziites reitzi* Zone. Because this level can be also recognized by ammonoids, conodonts and sporomorphs, there is no reason to change this priority base of the Ladinian to any other level. This priority remained unchanged for about 100 years. Even those proposals in the end of the last century that placed the Anisian-Ladinian boundary between the *Paraceratites trinodosus* Zone and the *Eoprotrachyceras curionii* Zone, in reality used the base of the *Reitziites reitzii* Zone as base of the Ladinian (in this time still named as Norian) because in the *"Trachyceras" curionii* Zone the *"Ceratites" reitzi* Zone was included as the lowermost horizon (see KOZUR & MOSTLER, 1994).

Within the Tethyan Ladinian, advanced oertlispongids are common in all stratigraphic levels. The evolution of these forms is very rapid and allows detailed subdivisions and correlations. Only few advanced oertlispongids are known from the Cordevolian, where they are replaced by their successors, the parasaturnalids (*Paleosaturnalis*).

Many new taxa of advanced oertlispongids have been described from the Early Ladinian in KOZUR & MOSTLER (1994). In the present paper several new taxa are described from the Longobardian. The present material was derived from the Dinarides of the Republic Bosnia-Hercegovina at the locality Varoški creek, about 2 km W of Fojnica (Geological Map 135 GACKO 1: 50 000) that was described by MURGENOVIĆ & ĞAKOVIĆ (1964). This locality is situated south of Sarajevo near the road Mostar-Gacko. The material (insoluble residues of limestone solved in acetic acid) was given to us by L. KRYSTYN, Vienna. His sample no. is 88/272. The age determination was originally based on the radiolarian fauna that is characteristic of the lower part of the upper Subzone (*Spongoserrula fluegeli* Subzone) of *Muelleritortis cochleata* Zone indicating an early late Longobardian age. Later, we recovered in the voluminous insoluble residues *Budurovignathus mungoensis* (DIEBEL), the conodont index species of the middle to late Longobardian *B. mungoensis* Zone.

Material of the lower and middle subzones of the *M. cochleata* Zone (*Pterospongus priscus*- and *Spongoserrula rarauana* subzones) have been investigated from the Karawanken (Southern Alps, samples St 1 and Bi 1, locality data see MOSTLER & KRAINER 1994). Material from the middle subzone and the lower part of the upper subzone of the *M. cochleata* Zone was investigated in Hungary (section Köveskál, locality data see KOZUR & MOSTLER, 1994). Oertlispongidae from the upper part of the upper Subzone of *M. cochleata* Zone and from the early Cordevolian have been studied from the section Dallapuszta (northern Hungary). These rich radiolarian faunas from red radiolarite blocks in a Middle Jurassic to Oxfordian accretionary complex of the Meliaticum are unfortunately rather fragmentary preserved. Late Cordevolian Oertlispongidae have been studied from a section about 500 m south of Pietra dei Saracini in the Sosio Valley area, western Sicily (Italy).

2. Systematic part

If not otherwise indicated, the described and figured material is form radiolarian-bearing micritic limestones of the locality Varoški creek. It is the type locality for all new species, where no type locality is indicated. The limestone was a floated block of a radiolarian-bearing limestone with an intercalation of tuffitic shales and radiolarites (see Fig. 2). The material is deposited in the Institute of Geology and Paleontology, Innsbruck University, if not otherwise indicated.

Subclass Radiolaria MÜLLER, 1858
Order Polycystina EHRENBERG, 1838
Suborder Spumellaria EHRENBERG, 1875
Superfamily Sponguracea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1981

Family Oertlispongidae KOZUR & MOSTLER, 1980

Subfamily Oertlisponginae
KOZUR & MOSTLER, 1980

Description: Spongy shell consisting of 5–7 concentric shells around a tiny microsphere. One or two polar spines are present. One of them (main polar spine) is recurved at one side or at two sides, exceptionally at three sides in triangular position. The recurved end(s) may join the shell. The main polar spine is often strongly differentiated to a blade-like shape. It may be smooth or with denticles or rounded appendages on its outer margin. The most primitive ancestral forms (*Paroertlispongus*) display a straight, also distally not curved main polar spine with circular outline. But even in these forms the main polar spine may be differentiated (e.g. by a small, flat lobe). The second polar spine (if present) is needle-like and mostly long. Further needle-like by spines may be present in the antapical hemisphere of the spongy shell. They are often arranged in a bunch.

Assigned genera:
Oertlispongus DUMITRICĂ, KOZUR & MOSTLER, 1980

Baumgartneria DUMITRICĂ, 1982
Falcispongus DUMITRICĂ, 1982
Pterospongus DUMITRICĂ, 1982
Spongoserrula DUMITRICĂ, 1982
Paroertlispongus KOZUR & MOSTLER, 1981
Angulocircus LAHM, 1984
Bogdanella KOLAR-JURKOVŠEK, 1989
Turospongus KOZUR & MOSTLER, 1994
Gibberospongus n. gen.
Scutispongus n. gen.
Steigerispongus n. gen.

Occurrence: Illyrian (only primitive forms without recurved differentiated main polar spine), Ladinian-Cordevolian. Very common in the Tethys, rare in the Circum-Pacific realm.

Remarks: The Intermediellinae LAHM, 1984, display three main spines in triangular position.

At the base of the Carnian the saturnalid Parasaturnalidae KOZUR & MOSTLER, 1972, evolved from Oertlisponginae. *Angulocircus* LAHM (1984) is a transitional form, in which the saturnalid ring is not yet closed (see KOZUR & MOSTLER, 1990).

Genus *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Type species: *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Oertlispongus inaequispinosus DUMITRICĂ, KOZUR & MOSTLER, 1980
(Pl. 14, Figs. 10, 11)

1980 *Oertlispongus inaequispinosus* n. sp. – DUMITRICĂ, KOZUR & MOSTLER, p. 5, Pl. 10, Fig. 7
1982 *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER – DUMITRICĂ, p. 64–65, Pl. 1, Figs. 6, 7, 9, non! Figs. 2, 4
1982 *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER – DUMITRICĂ & MELLO, Pl. 2, Figs. 1, 2

1984 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER – LAHM, p. 48, Pl. 8, Fig. 2

1986 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER - KOZUR & RÉTI, Fig. 5

1989 *Oertlispongus inaequispinosus* KOZUR &
MOSTLER (sic!) – MARTINI et al., Pl. 3,
Fig. 14

1990 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER – GORIČAN & BUSER, p.
148–149, Pl. 3, Figs., 10, 11

1990 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR and MOSTLER – YEH, p. 16, Pl. 4, Fig. 1

1990 *Oertlispongus inaequispinosus* KOZUR &
MOSTLER (sic!) – DE WEVER, MARTINI &
ZANINETTI, Pl. 1, Fig. 16

1993 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER – DOSZTÁLY & JÓZSA,
Pl. 1, Fig. 5

1994 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER – DOSZTÁLY, Pl. 2,
Figs. 7, 8, non! Figs 3–6

1994 *Oertlispongus inaequispinosus* DUMITRICĂ,
KOZUR & MOSTLER – KOZUR & MOSTLER,
p. 59, Pl. 10, Figs. 1–4, 5 (?), 6, 7, 11, 13,
Pl. 11, Figs. 2, 6, 7, 9, 11 (?); Pl. 47, Figs. 6, 7

Occurrence: Common from the middle *Reitziites
reitzi* Zone to *Eoprotrachyceras curionii* Zone, rare
in the early and middle Longobardian. Tethys and
Circum-Pacific realm. One of the best guide forms
for Ladinian age (see KOZUR & MOSTLER, 1994).

Remarks: The taxonomy of *Oertlispongus inae-
quispinosus* DUMITRICA, KOZUR & MOSTLER,
1980 was discussed in detail by KOZUR & MOST-
LER (1994). Several subspecies have been discrim-
inated. Forms with long, straight stem were separ-
ated as independent species. For details of taxono-
my see KOZUR & MOSTLER (1994).

Oertlispongus deweveri n.sp
(Pl. 7, Fig. 5)

Derivation of name: In honour of Dr. P. DE
WEVER, Paris.
Holotype: The specimen on Pl. 7, Fig. 5; rep.-no.
KOMO 1994 IV-1

Material: 6 specimens.
Diagnosis: Main polar spine clothes hook-shap-
ed. Straight stem narrow, moderately long. The
main polar spine is broadest in the turning point of
the curve.
Measurements:
Length of straight stem above the shell surface:
65–70 µm
Total length of the main polar spine above the shell
surface: 160–165 µm
Occurrence: Stratigraphically youngest repre-
sentative of the genus *Oertlispongus*. Rare in the
lower *Spongoserrula fluegeli* Subzone of the
Muelleritortis cochleata Zone (early late Longo-
bardian) at the type locality.
Remarks: The clothes-hook shaped main polar
spine is very different from all other (Early Ladin-
ian) *Oertlispongus* species which are curved in
one direction.

Genus *Baumgartneria* DUMITRICĂ 1982

Type species: *Baumgartneria retrospina* DUMIT-
RICĂ, 1982

Baumgartneria curvispina DUMITRICĂ, 1982
(Pl. 14, Figs. 8, 9, 12)

1982 *Baumgartneria curvispina* n. sp. – DUMIT-
RICĂ, p. 71, Pl. 12, Figs. 1, 2, 4
Occurrence: *Pterospongus priscus*- and *Spon-
goserrula rarauana* subzones of *Muelleritortis
cochleata* Zone (middle Longobardian) of the Te-
thys.
Remarks: *Baumgartneria curvispina* DUMITRI-
CĂ, 1982 is the forerunner of *Pterospongus* DU-
MITRICĂ, 1982. The transition forms are described
in the present paper (*Pterospongus priscus* n. sp.).

Baumgartneria curvispina DUMITRICA, 1982, is
not more a typical *Baumgartneria*, because oppo-
site to the stem a very small, moderately flattened
blade-like part is present. It is not the type species
of *Baumgartneria* DUMITRICĂ, 1982, as errone-

ously designated by DE WEVER (1984, p. 303, by misspelling named as *Baumgartneria curvispinata* DUMITRICĂ). There are two morphotypes in *Baumgartneria curvispina*, already figured in DU-MITRICĂ (1982). Morphotype 1 displays a semi-elliptical or rounded subtriangula small blade above the stem. To this morphotype belongs the holotype and the specimen figured on Pl. 14, Fig. 12). Morphotype 2 displays a straight or very slightly concave portion opposite to the stem (Pl. 14, figs. 8, 9). In this morphotype a bladelike portion at the branching point stem-open ring is missing. This latter morphotype is the ancestral form of *Pterospongus priscus* n. sp. Perhaps these two morphotypes represent independent subspecies.

Genus *Falcispongus* DUMITRICĂ, 1982

Type species: *Falcispongus falciformis* DUMITRI-CĂ, 1982

Falcispongus falciformis minor n. subsp.
(Pl. 14, Fig. 4)

Derivation of name: According to the small size of the polar spine.
Holotype: The specimen on Pl. 14, Fig. 4; rep.-no. KOMO 1994 IV-173
Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).
Type stratum: Middle part of Buchenstein Beds, sample St 1.
Material: 6 specimens.
Diagnosis: Spongy shell and spine rather small. Stem moderately long, narrow. Blade rather broad, semielliptical to semicircular in outline, present only on the outer side of the spine. The distal portion of the polar spine is strongly backward curved (nearly parallel to the stem).
Measurements:
Length of polar spine above the shell surface: 117–128 μm

Maximum width of polar spine (maximum distance between the inner and outer margins of the blade): 60–62 μm
Length of straight stem above the shell: 39–44 μm
Width of straight stem in its middle part: 25–27 μm
Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality. Rare in the early Cordevolian of Hungary.
Remarks: *Falcispongus falciformis falciformis* DUMITRICĂ, 1982, is considerably larger, the blade is present at the outer and inner side of the spine and the distal part of the spine is obliquely backward directed and not so strong backward curved as in *F. falciformis minor* n. subsp.

Falcispongus hamatus DUMITRICĂ, 1982, corresponds in size and strongly backward curved polar spine to *Falcispongus falciformis minor* n. subsp. However, the straight stem is very short or absent above the shell. Moreover, the shape of the blade is triangular, widest near to its proximal end.

Falcispongus hamatus DUMITRICĂ, 1982
(Pl. 9, Figs. 1, 5; Pl. 14, Figs. 2, 3)

1982 *Falcispongus hamatus* n. sp., pars – DUMIT-RICĂ, p. 66–67, only the specimen on Pl. 3, Fig. 1
1990 *Falcispongus hamatus* DUMITRICĂ, 1982 a – GORIČAN & BUSER, p. 145, Pl. 3, Fig. 7
Occurrence: The holotype was derived from the Tuvalian according to DUMITRICĂ (1982). However, we could not find this species in beds younger than Cordevolian.
Remarks: The holotype displays a subtriangular blade, widest at its proximal end, where it has a slightly concave external margin. Several specimens have a semielliptical blade with convex external margin (Pl. 9, Fig. 5, and the specimen figured by GORIČAN & BUSER, 1990). The width of the blade is variable. Specimens with very narrow blade are assigned herein to *Falcispongus* cf. *hamatus* DUMITRICĂ, 1982 (Pl. 14, Fig. 1). They are transition forms to advanced *Oertlispongus inae-*

quispinosus Dumitrică, Kozur & Mostler, 1980. The main difference to *Falcispongus falciformis* Dumitrică, 1982 is the length of the stem above the shell and the stronger backward curved spine. Moreover, as already stated by Dumitrică (1982), the size of typical *Falcispongus falciformis* is distinctly larger than in *Falcispongus hamatus*. However, in the early Longobardian and early middle Longobardian, a new subspecies of *Falcispongus falciformis* occurs that is as small as *Falcispongus hamatus*. The stem is moderately long to long in *F. falciformis*, but very short or missing in *F. hamatus*

Falcispongus transitus n. sp.
(Pl. 8, Fig. 3; Pl. 9, Figs. 4, 10, 13, 14;
Pl. 13; Fig. 5; Pl. 14, Fig. 5)

1982 *Falcispongus hamatus* n. sp., pars – Dumitrică, p. 66–67, only the specimen on Pl. 3, Fig. 4

Derivation of name: According to the transitional character between the genera *Falcispongus* Dumitrică, 1982 and *Gibberospongus* n. gen.

Holotype: The specimen on Pl. 9, Fig. 13; rep.-no Komo 1994 IV-5

Material: 103 specimens.

Diagnosis: Globular spongy shell with tiny, irregularly distributed by-spines. Straight stem of the polar spine outside the shell absent or very short. Immediately above the shell the polar spine is blade-like widened. This blade is of about the same width throughout its length, in typical specimens long, in primitive forms rather short. Its external margin is slightly convex or straight, its inner margin slightly concave. Its distal end is broadly rounded and mostly a little expanded, but not in form of an appendage. The spine is included into the inner margin of the blade. Its free part is narrow and strongly recurved. Its length is variable.

Measurements: See under the subspecies.

Occurrence: Common in the lower and middle subzones of *Muelleritortis cochleata* Zone (middle Longobardian) of Southern Alps, Romania and Bosnia-Hercegovina.

Remarks: *Falcispongus transitus* n. sp. is the ancestor of *Gibberospongus* n. gen. In *Falcispongus* aff. *F. transitus* (Pl. 8, Fig. 2) the distal expansion of the blade becomes larger. Such forms are very similar to *Gibberospongus kraineri* n. sp. that displays a cylindrical appendage at the outer distal corner of the blade.

In *Falcispongus* cf. *transitus* n. sp. there is no distal expansion. This form is somewhat similar to *Falcispongus hamatus* Dumitrică, 1982, in which, however, the width of the blade gradually decreases from its widest part near the proximal end in distal direction.

The holotype of *Falcispongus hamatus* Dumitrică, 1982 displays a subtriangular blade that is in the distal part distinctly narrower than in the proximal part. The two other specimens assigned by Dumitrică (1982) to *Falcispongus hamatus* do not belong to this species. One of them (Dumitrică, 1982, Pl. 3, Fig. 4) belongs to *Falcispongus transitus* n. sp., the other one (Dumitrică, 1982, Pl. 4, Fig. 1) is a *Falcispongus rostratus* Dumitrică, 1982.

Falcispongus transitus transitus n. subsp.
(Pl. 9, Figs. 4, 10, 13, 14)

Holotype: = holotype of the species.

Material: 54 specimens.

Diagnosis: With the character of the species. Blade long, mostly relatively narrow, distally somewhat expanded.

Measurements:

Length of polar spine above the shell surface: 130–171 µm

Length of blade: 145–176 µm

Maximum width of polar spine: 45–83 µm

Length of straight stem: 0–12 µm

Width of straight stem: 23–35 µm

Length of the recurved part of the polar spine: 145–294 µm

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Falcispongus transitus brevifoliaceus n. subsp.
(Pl. 8, Fig. 3; Pl. 13, Fig. 5; Pl. 14, Fig. 5)

Derivation of name: According to the short blade.
Holotype: The specimen on Pl. 8, Fig. 3; rep.-no. KOMO 1994 IV-8
Material: 47 specimens.
Diagnosis: With the character of the species. Blade short and relatively to its length broad.
Measurements:
Diameter of spongy shell: 78–111 μm
Length of polar spine above the shell surface: 100–130 μm
Length of blade: 108–120 μm
Maximum width of polar spine: 55–61 μm
Length of straight stem above the shell: 0–10 μm
Width of straight stem: 25 μm
Length of recurved part of polar spine: 175–277 μm
Occurrence: Common in the lower subzone (*Pterospongus priscus* Subzone) of the *Muelleritortis cochleata* Zone (early middle Longobardian) and rare in the lower *Spongoserrula fluegeli* Subzone of *M. cochleata* Zone (early late Longobardian) of Southern Alps and Bosnia-Hercegovina.
Remarks: See also under the species.

Falcispongus transitus transitus n. subsp. displays a longer blade.

Genus *Pterospongus* DUMITRICA, 1982

Type species: *Pterospongus patrulii* DUMITRICĂ, 1982

Pterospongus alatus DUMITRICĂ 1982
(Pl. 15, Fig. 1)

1982 *Pterospongus alatus* n. sp. – DUMITRICĂ, p. 69, Pl. 4, Fig. 7, Pl. 5, Fig. 3, non! Fig. 1
Material: 3 specimens.
Occurrence: *Pterospongus priscus-* and *Spongoserrula rarauana* subzones of *Muelleritortis cochleata* Zone (middle Longobardian) of Romania, Hungary and Southern Alps.

Remarks: *Pterospongus alatus* DUMITRICĂ, 1982 evolved from *Pterospongus priscus* n. sp. by development of a larger, symmetrical blade with broad and moderately deep apical incision.

Our material from the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) belongs probably to a new subspecies. Typical forms from the *Spongoserrula rarauana* Subzone of *Muelleritortis cochleata* Zone (middle Longobardian) displays a horizontally wider and generally higher blade. Probably the terminal spines of the wings are shorter. However, these terminal spines are neither in the type material (DUMITRICĂ, 1982) nor in our material fully preserved. For this reason and for the fact that neither in the type material nor in our material the intraspecific variability is well known, we do not establish this new subspecies before further material is known.

Pterospongus altofissus n. sp.
(Pl. 15, Figs. 4, 5)

Derivation of name: According to the deep apical incision.
Holotype: The specimen on Pl. 15, Fig. 5; rep.-no. KOMO 1994 IV-191
Material: 5 specimens.
Diagnosis: Stem short to moderately long, narrow. Blade large, high, bilateral, asymmetrical. At one side, the transition to the short-moderately long terminal spine of the wing is gradual. At the other side, the blade becomes abruptly narrower at the base of the terminal spine. Incision narrow to moderately broad, deep.
Measurements:
Length of polar spine above the shell surface: 213–242 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 100–142 μm
Length of straight stem above the shell: 75–87 μm
Width of straight stem in its middle part: 23–27 μm

Length of terminal spines of the wings: Maximally 100 µm

Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of the *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: The blade of *Pterospongus incissus* DUMITRICĂ, 1982 is symmetrical, but otherwise similar (large, high, with deep apical incision). However, the straight stem above the shell is either very short or absent. The contemporaneous species *Pterospongus parvifissus* n. sp. and *P. priscus* n. sp. have not a high blade and their apical incision is considerably shallower.

Pterospongus parvifissus n. sp.
(Pl. 14, Fig. 16; Pl. 15, Figs. 2, 3)

Derivation of name: According to the small incision.

Holotype: The specimen on Pl. 14, Fig. 16; rep.-no. KOMO 1994 IV-184

Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).

Type stratum: Middle part of Buchenstein Beds, sample St 1.

Material: 43 specimens.

Diagnosis: Straight stem of polar spine moderately long, narrow. Blade small and low to moderately high, horizontally short, with narrow, moderately deep incision. Terminal spines very long, backward, in the distal part also curved inwards. They form an antapically open elliptical ring with the spongy shell in the centre.

Measurements:

Diameter of spongy shell: 113–150 µm

Length of polar spine above the shell surface: 166–176 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 61–80 µm

Length of straight stem above the shell: 73–106 µm

Width of straight stem in its middle part: 26–33 µm

Length of terminal spines of the wings: up to 335 µm (mostly not fully preserved)

Occurrence: Common in the lower subzone (*Pterospongus priscus* Subzone) of the *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: *Pterospongus alatus* DUMITRICĂ, 1982, is distinguished by a longer and higher blade and a much wider apical incision. Moreover, the terminal spines of the blade do not form an antapically open ring. The few specimens from the lower subzone (*Pterospongus priscus* Subzone) of the *Muelleritortis cochleata* Zone (early middle Longobardian) display a short blade and are therefore similar to *Pterospongus parvifissus*. They are distinguished from this species by a wide apical incision and obliquely backward directed terminal spines of the wings.

Pterospongus priscus n. sp. displays a low blade with wide, shallow, often indistinct apical incision.

Pterospongus priscus n. sp.
(Pl. 14, Figs. 13, 14, 17, 18)

Derivation of name: Stratigraphically earliest known *Pterospongus*.

Holotype: The specimen on Pl. 14, Fig. 14; rep.-no. KOMO 1994 IV-183

Material: 65 specimens.

Diagnosis: Stem of polar spine moderately long, narrow. Blade low, rather short, slightly asymmetric, with wide, but shallow and sometimes indistinct apical incision. The platform portions at the end of the incision may be twisted against each other (at one side upward bent, on the other side downward bent). The very long terminal spines of the wings are backward curved and form an apically open, elliptical or subcircular ring with the shell in the centre.

Measurements:

Diameter of spongy shell: 100–127 µm

Length of polar spine above the shell surface: 133–153 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 47–67 µm

Length of straight stem above the shell: 67–106 μm
Width of straight stem in its middle part: 21–23 μm
Length of the terminal spines of the wings: > 235 μm (not fully preserved)

Occurrence: Common in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality and in Hungary.

Remarks: In *Pterospongus parvifissus* n. sp. the blade is higher. The apical incision is narrower, but deeper.

Pterospongus priscus n. sp. is a transition from between *Baumgartneria* DUMITRICĂ, 1982 of *B. curvispina* group and *Pterospongus* DUMITRICĂ, 1982, of *P. alatus* group. The terminal spines of the wings form an antapically open ring as in *Baumgartneria curvispina*. However, there is a distinct blade with an apical incision as in all *Pterospongus* species. In some specimens of *Baumgartneria curvispina* DUMITRICĂ, 1982 a very small blade may be present, but an apical incision is absent.

Pterospongus priscus priscus n. subsp.
(Pl. 14, Figs. 13, 14)

Holotype: = holotype of the species.
Material: 53 specimens.
Diagnosis: With the character of the species. The blade portions at the ends of the incision are not twisted against each other.
Measurements: As for the species.
Occurrence: Common in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality and in Hungary.

Pterospongus priscus tortilis n. subsp.
(Pl. 14, Figs. 17, 18)

Derivation of name: According to the twisted blade.
Holotype: The specimen on Pl. 14, Fig. 18; rep.-no. KOMO 1994 IV-186

Material: 12 specimens.
Diagnosis: With the character of the species. The blade portions adjacent to the incision are twisted against each other. At one side of the incision, the blade is upward, on the other side downward curved.
Measurements: As for the species.
Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.
Remarks: See also under the species.

In *Pterospongus priscus priscus* n. sp. the blade is not twisted.

Genus *Spongoserrula* DUMITRICĂ, 1982

Type species: *Spongoserrula rarauana* DUMITRICĂ, 1982
Occurrence: Longobardian and Cordevolian. Very common in the Tethys, rare to common in the Circum-Pacific realm (Philippines and British Columbia, Canada). The occurrence in the Tuvalian mentioned by DUMITRICĂ (1982) could not be confirmed.
Remarks: DUMITRICĂ (1982) assigned to *Spongoserrula* two species, the type species *S. rarauana* DUMITRICĂ and *S. cristagalli* DUMITRICĂ. Both species display a completely flattened polar spine with rounded or blunt flattened subcylindrical spines at the external margin. However, in the type species *S. rarauana* the blade-like polar spine is sickle-shaped, recurved only to one side. In *S. cristagalli* the straight stem is long and the blade-like polar spine is bilateral with distal recurving on both sides. This species belong to a new genus, *Steigerispongus* n. gen., which is distinguished from *Pterospongus* DUMITRICĂ, 1982 by the missing distinct incision opposite to the stem of the polar spine. Moreover, most, but not all *Steigerispongus* species are asymmetric, whereas *Pterospongus* is symmetric.

All transitions from *Falcispongus* to *Spongoserrula* have been observed in our material. The most primitive *Spongoserrula*, *S. nuda* n. sp. and

S. antiqua n. sp., display a sickle-shaped main spine with a smooth external margin. They are distinguished from *Falcispongus* by the completely flattened, blade-like spine which is, however, narrow. In the likewise sickle-shaped, but somewhat broader *Spongoserrula falcata* n. sp., some undulations on the external margin indicate the beginning of the denticulation of the external margin. The most primitive forms with denticles on the external margin of the blade display only a few, very short semicircular or rounded triangular to short-subcylindrical denticles. Typical *Spongoserrula* display numerous, long, flattened cylindrical spines with blunt or rounded ends. A group with long pointed spines evolved from these forms. Transitional forms to *Steigerispongus* n. gen. display a large proximal denticle which is directed opposite to the recurved distal end. In *Steigerispongus* n. gen., this spine becomes longer, broader, recurved and on the external margin spiny. By this, it is transformed in a second recurved branch of blade that becomes finally as large as the primary branch to form more symmetrical blades with recurvation on both sides.

Spongoserrula rarauana rarauana
DUMITRICĂ, 1982
(Pl. 5, Figs. ? 10, 11, 13–15;
Pl. 6, figs. 1–3, 6, 9; Pl. 8, Fig. 9)

1982 *Spongoserrula rarauana* n. sp. – DUMITRI-
CĂ, p. 67, Pl. 5, Fig. 5–7; Pl. 6, Figs. 1–5;
Pl. 12, Figs. 10–13; non! Pl. 7, Fig. 4
1990 *Spongoserrula rarauna* (sic!) DUMITRICĂ-
DOSZTÁLY, p. 69, Pl. 1 Fig. 2
1994 *Spongoserrula rarauna* (sic !) DUMITRICĂ -
DOSZTÁLY, p. 63, Pl. 1 Fig. 6
1994 *Spongoserrula rarauna* (sic !) DUMITRICĂ -
DOSZTÁLY, Pl. 1, Fig. 6

Description: Globular spongy shell with a big, blade-like polar spine and several small, needle-like by-spines which are concentrated to the hemisphere opposite to the main spine. A part of them is arranged in a bunch in some distance from the antapical pole. The polar spine widens

considerably after a short, distally widened stem. In the level of the largest widening, a heel-shaped lobe is present on the external margin. After this lobe the blade becomes gradual and slowly narrower toward the distal end; the distal, undenticulated part of the polar spine is narrow, needle shaped, moderately recurved. The distal end of the polar spine lies about in the level of the shell equator. Exceptionally, it joins the shell. On the external margin of the polar spine 4–7 flattened subcylindrical, distally rounded or blunt denticles are present. The proximal denticles are long; their length is decreasing in distal direction. Exceptionally, all denticles have the same length (Pl. 5, Fig. 11). The moderately long, needle-shaped distal part of the polar spine is undenticulated.

Occurrence: Middle late Longobardian. Tuvalian occurrences, reported by DUMITRICĂ (1982) cannot be confirmed.

Remarks: Specimens with 3 short node-like to rounded subtriangular appendages at the external margin of the blade-like polar spine are separated as an independent subspecies. These forms have a sickle-shaped, blade-like polar spine without lobe and the blade is not significantly broadened above the stem. They are transitional forms from *Spongoserrula falcata* n. sp. to *S. rarauana rarauana* DUMITRICĂ.

DUMITRICĂ (1982) correctly mentioned that the teeth have blunt tips. Later authors assigned forms with needle-shaped teeth and pointed tips into *S. rarauana* (DE WEVER, 1984, CORDEY et al., 1988, DOSZTÁLY, 1991). These forms, however, belong to an independent species which has a narrower blade without lobe.

Spongoserrula rarauana trinodosa n. subsp.
(Pl. 5, Fig. 8, 12; Pl. 12, Fig. 3)

Derivation of name: According to the three node-like elevations on the external margin of the polar spine.

Holotype: The specimen on Pl. 5, Fig. 8; rep.-no. KOMO 1994 IV-36
Material: 15 specimens.

Diagnosis: Spongy shell with few tiny by-spines. Polar spine completely flattened, sickle-shaped, narrow for the genus. The stem is short and as wide as the widest part of the polar spine or only a little narrower. Its distal end is moderately long, needle-shaped, strongly recurved. External margin in the middle part of the polar spine with three node-like, rounded subtriangular to flattened subcylindrical denticles.

Measurements:

Diameter of shell: 118–154 μm

Length of polar spine above the shell surface (without nodes): 126–192 μm

Maximum width of polar spine: 63–88 μm

Length of recurved part of polar spine: 206–257 μm

Maximum length of nodes: 23 μm

Occurrence: *Spongoserrula rarauana* Subzone and lower *S. fluegeli* Subzone of *Muelleritortis cochleata* Zone (middle to early late Longobardian) of Bosnia-Hercegovina and Hungary.

Remarks: *Spongoserrula rarauana trinodosa* n. subsp. is a transition form between *S. falcata* n. sp. and *S. rarauana rarauana* DUMITRICĂ, 1982. The first species displays the same shape of the polar spine that is in the same manner curved. However, the external margin of the polar spine is only slightly undulated and it bears never nodes. The polar spine of *S. rarauana rarauana* is strongly widened, bears more denticles and in the proximal part on the external margin a heel-shaped lobe. Some specimens of *S. rarauana trinodosa* (Pl. 5, Fig. 12) display an indistinct, small, subtriangular lobe and the three denticles are elongated node-like (maximum length 29 μm). The polar spine is, however, nearly as narrow as in typical *S. rarauana trinodosa*. These forms are transition forms to *S. rarauana rarauana*. Among this latter subspecies transition forms are rarely present as well (*S.* cf. *rarauana rarauana*, Pl. 5, Fig. 15). In these forms the widening of the polar spine is only somewhat stronger than in typical *S. rarauana trinodosa* and the lobe is small and indistinct. But there are already 3 flattened subcylindrical teeth (maximum length 47 μm) and a fourth small rounded subtriangular denticle.

Spongoserrula cf. *rarauana trinodosa* (Pl. 12, Fig. 2) displays additionally to the three small node-like denticles one or two broadly node-like to lobe-like undulations. The blade has the same shape as in *S. rarauana trinodosa*.

Spongoserrula cf. *dehli* CORDEY, F., DE WEVER, P., DUMITRICĂ, P., DANELIAN, T., KITO, N. & VRIELYNCK, B., 1988
(Pl. 13, Fig. 8)

1988 *Spongoserrula dehli* n. sp. – CORDEY et al., p. 31–32, Pl. 1, Figs. 1–5

Occurrence: Cordevolian of North America and Sicily. CORDEY et al. (1988) assigned this fauna to the late Anisian to Early Ladinian. However, the association with *Tritortis kretaensis kretaensis* (KOZUR & KRAHL, 1984) and *Spongoserrula dehli* CORDEY et al. occurs in Sicily in Cordevolian beds with *Paragondolella polygnathiformis* (BUDUROV & STEFANOV) and other Carnian guideforms. *Tritortis kretaensis kretaensis* did not appear before the late Longobardian and *Spongoserrula dehli* was so far only found in Cordevolian beds.

Remarks: *Spongoserrula dehli* CORDEY et al. (1988) belongs to the late Longobardian-Cordevolian *Spongoserrula fluegeli* group that is characterized by pointed, often needle-like denticles. *Spongoserrula fluegeli* n. sp. is very similar, but the large proximal spine is in this species always upside convex. The direction of this denticle is variable, mostly obliquely downward directed, but also perpendicularly to the stem or obliquely upward directed. The proximal spine of *S. dehli* is always slightly to distinctly upside concave and nearly perpendicularly to the stem or (mostly) obliquely upward directed.

In the figured specimen a somewhat smaller denticle is intercalated between the two largest proximal teeth. Therefore the distance between the first three proximal teeth is rather small compared with typical *Spongoserrula dehli*. Because only one specimen of this type is present, we assign this form to *Spongoserrula* cf. *dehli*. It may be, however, described as an independent subspecies, if more material can be found.

The forerunner of typical *Spongoserrula dehli* CORDEY et al., 1988 is known from the *Spongoserrula rarauana* Subzone of Hungary. In this form the first proximal spine is basally broad, but considerably shorter than the first proximal spine in *Spongoserrula dehli*, but also upside concave. The denticulation is similar to *Spongoserrula dehli* n. sp., but in this species the first proximal denticle is needle-like and straight.

Spongoserrula antiqua n. sp.
(Pl. 14, Figs. 6,7)

Derivation of name: Stratigraphically oldest species of *Spongoserrula*.
Holotype: The specimen on Pl. 14, Fig. 6; rep.-no. KOMO 1994 IV-175
Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).
Type stratum: Middle part of Buchenstein Beds, sample St 1.
Material: 5 specimens.
Diagnosis: Spongy shell with few, needle-like, short by-spines, irregularly distributed over the entire shell surface. Antapical polar spine needle-shaped, rather long. Main (apical) polar spine completely flattened, sickle-shaped. Straight stem above the shell very short or absent. Distal part of the polar spine moderately curved backwards.
Measurements:
Length of polar spine above the shell surface: 107–113 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 47 67 μm
Length of straight stem above the shell: 0–20 μm
Width of straight stem: 33–43 μm
Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.
Remarks: *Spongoserrula nuda* n. sp. displays a considerably longer straight portion of the polar

spine that is therefore considerably higher. Both species are completely undenticulated.

Spongoserrula falcata n. sp. displays a broader blade with undulated external margin. This species is the transition form between *Spongoserrula antiqua* n. sp. with completely smooth blade and denticulated typical *Spongoserrula* of the *S. rarauana* group.

In *Falcispongus* DUMITRICĂ, 1982 only the blade is flattened, whereas the spine remain circular in cross section. *Spongoserrula antiqua* n. sp. is therefore the link between *Falcispongus* and *Spongoserrula*.

Spongoserrula bidentata n. sp.
(Pl. 5, Fig. 9; Pl. 12, Fig. 5)

1982 *Spongoserrula rarauana* n. sp., pars - DUMITRICĂ, p. 67, only the specimen on Pl. 7, Fig. 4
Derivation of name: According to the presence of two, rather long denticles at the external margin of the blade-like polar spine.
Holotype: The specimen on Pl. 5, Fig. 9; rep.-no. KOMO 1994 IV-41
Material: 7 specimens.
Diagnosis: Polar spine completely flattened, moderately broad, blade-like. Straight stem very short, with gradual transition to the blade-like broadened part of the polar spine. Heel-like lobe on the external margin of the proximal blade distinct, but not high. On the upper external margin of the blade two widely separated, diverging, flattened subcylindrical denticles with rounded or blunt ends are present. At the base of the moderately long, needle-like distal spine an undulation or small, rounded triangular lobe may be present, which corresponds to a third denticle. The terminal spine is moderately recurved and ends somewhat above the upper pole of the shell. Sometimes its distal end is upward curved.
Measurements:
Length of polar spine above the shell surface (without denticles): 141–176 μm
Maximum width of polar spine: 82–132 μm

Length of recurved part of the polar spine: 145–178 μm
Maximum length of denticles: 24-72 μm

Occurrence: *Spongoserrula rarauana* Subzone and lower *S. fluegeli* Subzone of *Muelleritortis cochleata* Zone (middle to early late Longobardian) of Romania, Hungary and Bosnia-Hercegovina.

Remarks: *Spongoserrula rarauana* DUMITRICĂ, 1982 displays 4–7 denticles in specimens with likewise broad blade and likewise long denticles.

Spongoserrula bifurcata n. sp.
(Pl. 5, Figs. 4, 7; Pl. 13, Fig. 2)

Derivation of name: According to the bifurcated distal end of the polar spine.

Holotype: The specimen on Pl. 5, Fig. 7; rep.-no. KOMO 1994 IV-40

Material: 7 specimens.

Diagnosis: Spongy shell with several very small by-spines in the lower hemisphere. Antapical polar spine short, needle-like. Main (apical) polar spine completely flattened, broad to very broad, blade-like. Straight stem short. Heel-like lobe on the external margin of the proximal blade high. Three or four flattened subcylindrical denticles with rounded ends are present. Distal part of the polar spine very narrow, needle-like, moderately recurved. It ends in the level of the upper pole of the shell or a little above it. In its proximal part a short subtriangular spine or a shallow lobe is present. A second long, needle-like spine or short cylindrical spine branches off near the base of the terminal spine. This second terminal spine is either parallel to the stem or a little obliquely downward directed.

Measurements: See under the subspecies.

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: The only similar species is. *Spongoserrula ornata* n. sp. This species is distinguished by the presence of three needle-like terminal spines. Moreover, the denticles have the form of partly bifurcated large lobes.

Spongoserrula bifurcata bifurcata n. subsp.
(Pl. 5, Figs. 4, 7)

Holotype: = holotype of the species.
Material: 4 specimens.
Diagnosis: With the character of the species. There are 3 large denticles and a fourth small denticle on the proximal part of the outer terminal spine. The inner terminal spine is long and needle-like.

Measurements:
Length of polar spine above the shell surface (without denticles): 139–178 μm
Maximum width of polar spine: 106–128 μm
Length of straight stem above the shell surface: 44–50 μm
Length of recurved distal part of the polar spine: around 220 μm
Length of outer terminal spine: 160–166 μm
Length of inner terminal spine: 89–139 μm
Maximum length of denticles: 61–67 μm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: S
ee also under the species.

Spongoserrula bifurcata parvispina n. subsp. displays four denticles on the blade. The proximal part of the outer terminal spine has no denticle, but only a shallow lobe in the position of a denticle. The outer terminal spine is needle-like, but rather short. The inner terminal spine is very short, cylindrical.

Spongoserrula bifurcata parvispina n. subsp.
(Pl. 13, Fig. 2)

Derivation of name: According to the very smaller inner terminal spine.

Holotype: The specimen on Pl. 13, Fig. 2; rep.-no. KOMO 1994 IV-160

Material: 3 specimens.

Diagnosis: With the character of the species. The stem is rather long for the genus. The blade bears

four denticles. On the base of the outer terminal spine lies a shallow lobe in position of a further denticle. The outer terminal spine is needle-like, but short. The inner terminal spine is very short and narrow-cylindrical.

Measurements:

Length of polar spine above the shell surface (without denticles): 169–192 µm

Maximum width of polar spine: 111–119 µm

Length of straight stem above the shell: 54–61 µm

Width of straight stem in its middle part: 62 µm

Length of recurved distal part of the polar spine: 269–308 µm

Length of outer terminal spine: 106–110 µm

Length of inner terminal spine: 29–32 µm

Maximum length of denticles: 62–69 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Spongoserrula bifurcata bifurcata* n. subsp. displays only three denticles on the blade, but a fourth one on the proximal part of the outer terminal spine. Outer and inner terminal spines are long and needle-like.

Spongoserrula bipolaris n. sp.
(Pl. 6, Fig. 4; Pl. 12, Fig. 4)

Derivation of name: According to the bipolar arrangement of the two polar spines.

Holotype: The specimen on Pl. 6, Fig. 4; rep.-no. KOMO 1994 IV-44

Material: 12 specimens.

Diagnosis: Surface of the spongy shell with tiny spines and 1–3 very small, needle-like by-spines in the lower hemisphere. The antapical polar spine is long, needle-like, straight. The apical polar spine (main polar spine) is situated somewhat obliquely to the axis of the antapical polar spine. It is completely flattened, blade-like. In the widest part of the broad blade a rounded triangular to hemielliptical heel-like lobe is present on the external margin of the blade. The moderately recurved distal part of the main polar spine is needle-like, rather short. It ends in the level of the upper

pole of the shell or somewhat above it. The blade bears 3–4 denticles. The two proximal denticles are of nearly equal length. The following one is a little to distinctly shorter and the fourth denticle, if present, is always very small. The distal ends of the denticles are narrowly rounded, the two proximal denticles may be pointed, but not needle-like. The terminal spine-like end of the blade may display a little undulated external margin.

Measurements:

Diameter of shell: 107–130 µm

Length of main polar spine above the shell surface (without denticles): 143–207 µm

Maximum width of polar spine: 93–117 µm

Length of recurved part of the polar spine: 157–250 µm

Maximum length of denticles: 43-50 µm

Length of needle-like antapical polar spine: 243–257 µm

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: Most similar is *Spongoserrula rarauana* DUMITRICĂ, 1982, especially species with subtriangular heel-like lobe on the external side of the proximal blade (Pl. 6, Figs. 2, 6). *S. rarauana* has, however, more denticles with blunt to rounded ends. The spongy shell displays several needle-like by-spines, often arranged in a bunch in the shell half opposite to the flattened polar spine. A needle-like antapical polar spine is absent.

Spongoserrula cordeyi n. sp.

1984 *Spongoserrula rarauana* DUMITRICĂ, 1980 (sic!), pars – DE WEVER, p. 303, Pl. 1, Fig. 2 (?), 5 (most specimens are broken and indeterminable)

1988 *Spongoserrula rarauana* DUMITRICĂ – CORDEY et al., Pl. 1, Figs. 6, 7

Derivation of name: In honour of Dr. F. CORDEY, Vancouver

Holotype: The specimen figured in CORDEY et al. (1988, Pl. 1, Fig. 7 ; rep.-no. 85–311 (U.P.M.C. Paris)

Type locality: Southwest side of Harrison Lake, southern British Columbia, Canada (locality and sample data see CORDEY et al. (1988).

Type stratum: Siliceous argillite of the Camp Cove Formation, sample MV890. *Tritortis kretaensis* Zone.

Material: 43 broken specimens from the basal Cordevolian of Darnmple MV890. anada (locality andDiagnosis: Polar spine completely flattened to an unilateral sickle-shaped blade without separated stem above the shell surface. It is widest in its proximal third and becomes gradually narrower toward the distal end. No proximal lobe at the external margin. The 6–7 straight spines are proximally moderately long and their size gradually decreases toward the distal end of the blade. The spines are terminally needle-like, pointed, in the distal part of the blade more slender-triangular, but also pointed. The distance between the two proximal spines is considerably larger than the distances between the other spines.

Measurements:
Length of polar spine above the shell surface (without spines): 145–152 μm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 60–82 μm

Maximum length of spines: 50–74 μm

Occurrence: Common in the lower *Tritortis kretaensis* Zone of the Darnó-hegy area. *Tritortis kretaensis* Zone of British Columbia, Canada. This fauna was erroneously assigned to the Late Anisian-Early Ladinian by CORDEY et al. (1988), but *Tritortis kretaensis* (KOZUR & KRAHL, 1984) and *Spongoserrula* with pointed spines begin only in the late Longobardian and are still common in the Cordevolian *Tritortis kretaensis* Zone.

Remarks: As in the material figured by DE WEVER (1984) our radiolarian fauna from the Darnó-hegy consists mostly of broken specimens. All specimens of *Spongoserrula cordeyi* n. sp. are fragmentary. Therefore the holotype was chosen from the better preserved material figured by CORDEY et al. (1988).

Spongoserrula dehli CORDEY et al. (1988) displays considerably lager spines. The very large proximal spine is always upside concave.

In *Spongoserrula goricanae* n. sp. the distance between the spines is either equal on the entire blade or decreases gradually and slowly toward the distal end of the blade.

In *Spongoserrula fluegeli* n. sp. the proximal spine is distinctly longer than the following spines and the distances between the spines are either equal on the entire blade or decrease slowly and gradually toward the distal end of the blade. Moreover, the spines are generally more needle-like.

Spongoserrula falcata n. sp.
(Pl. 5, Figs. 2, 3, 5, 6)

Derivation of name: According to the sickle-shaped polar spine.

Holotype: The specimen on Pl. 5, Fig. 2; rep.-no. KOMO 1994 IV-32

Material: 34 specimens.

Diagnosis: Spongy shell small, with tiny spines. Polar spine completely flattened, sickle-shaped, narrow for the genus. Its proximal portion is short, flat and wide, its distal portion is needle-shaped, short to moderately long, moderately recurved. It ends in the level of the upper part of the shell or somewhat above it. The external margin of the middle part of the polar spine is slightly undulated, but nodes or spines are missing.

Measurements:
Diameter of shell: 95–112 μm

Length of polar spine above the shell surface: 115–171 μm

Maximum width of polar spine: 50–62 μm

Length of recurved part of the polar spine: 135–205 μm

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Spongoserrula falcata* n. sp. is a transition form between *Spongoserrula antiqua* n. sp. and *Spongoserrula trinodosa* n. sp. The first species has no undulations at the external margin of the polar spine. *Spongoserrula rarauana trinodo-*

sa n. subsp. has the same shape and degree of recurvation of the polar spine, but its external margin bears three nodes.

The straight proximal part of the polar spine in *S. nuda* n. sp. is longer and its distal end lies considerably above the shell. Moreover, this species displays a completely smooth outer margin of the blade without undulations.

Spongoserrula fluegeli n. sp.
(Pl. 6, Figs. 5, 7, 8, 10, 11)

Derivation of name: In honour of o. Univ. Prof. Dr. HELMUT FLÜGEL, Graz.

Holotype: The specimen on Pl. 6, Fig. 8; rep.-no. KOMO 1994 IV-45

Material: More than 100 specimens.

Diagnosis: Spongy shell with two polar spines. The antapical one is small, needle-like, straight. The main (apical) polar spine is completely flattened, blade-like, on the external side with 7-8 long, slender spines; rarely on the inner side a spine is present opposite to the last spine on the outer side. The straight stem is short. The blade is relatively narrow, widest in its proximal third. Toward the distal side its width slowly and gradually decreases. Distal part of the main polar spine needle-like, considerably recurved, without spines on its external margin. Its distal end lies in the level of the lower part of the shell or a little below the shell. The proximal spine on the external side is very large, needle-like. It is very slightly to distinctly convex. It may be obliquely upward directed, perpendicular to the polar axis or downward-recurved. Occasionally a small denticle is present on its outer side above in the mid-length of the spine. The following spines are large, but considerably smaller than the proximal spine. They are very slender, partly needle-like, with long, needle-like tips. Their length decreases slowly toward the distal end of the blade. The distances between the spines decrease gradually and slowly toward the distal end of the blade or are nearly equal on the entire blade.

Measurements:
Diameter of shell: 100–125 μm
Length of polar spine above the shell surface (without spines): 100–125 μm
Maximum width of polar spine: 50–69 μm
Length of recurved part of the polar spine: 263–333 μm
Length of proximal spine: 130–225 μm
Maximum length of other spines: 83–100 μm
Occurrence: Common in the late Longobardian of the Tethys.

Remarks: Most similar is *Spongoserrula dehli* CORDEY et al., 1988. In this species the proximal spine is also distinctly larger than the other ones, but it is always obliquely upward directed and upside concave. Moreover, there are fewer and wider separated spines on the external margin of the blade.

The *Spongoserrula fluegeli* group is the ancestral group of *Steigerispongus*. From the very large, convex and partly downward recurved proximal spine evolved in *Steigerispongus* a second, downward recurved blade with outer spines that is situated opposite to the primary recurved blade. In most species of *Steigerispongus*, this second blade is somewhat different from the primary recurved blade in form and its position to the stem. The beginning of this development is indicated in *Spongoserrula fluegeli multispinosa*, in which the big proximal spine displays a small denticle on its outer side. However, all *Steigerispongus* species have a long stem. Therefore, *Spongoserrula fluegeli* n. sp. is not the immediate ancestor of *Steigerispongus*, but rather a side branch, which indicates, however, the way, by which *Steigerispongus* evolved from *Spongoserrula*.

Spongoserrula fluegeli fluegeli n. subsp.
(Pl. 6, Figs. 5, 7, 8, 11; Pl. 13, Fig. 4)

Holotype, measurements and occurrence: As for the species.

Diagnosis: With the character of the species. Proximal spine without secondary denticle on its

external margin. Without spine at the inner margin of the blade.

Occurrence: Common in the *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (late Longobardian) of the Tethys.

Remarks: See also remarks to the species.

Spongoserrula fluegeli multispinosa displays a small denticle on the outer (upper) margin of the proximal spine. Moreover, a spine is present on the inner margin of the blade opposite to the smallest, distal outer spine of the blade.

Spongoserrula fluegeli multispinosa n. subsp.
(Pl. 6, Fig. 10)

Derivation of name: According to the numerous spines.

Holotype: The specimen on Pl. 6, Fig. 10; rep.-no. KOMO 1994 IV-49

Material: 2 specimens.

Diagnosis: With the character of the species. Proximal spine with a small denticle on its external (upper) margin about in the midlength of the spine. On the inner side of the blade a spine is present opposite to the smallest, distal spine on the exterior margin of the blade.

Measurements: As for the species.

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Spongoserrula fluegeli fluegeli* n. subsp. has no denticle on the external (upper) margin of the proximal spine and the inner margin of the blade has no denticle.

Spongoserrula goricanae n. sp.
(Pl. 13, Fig. 1)

1991 *Spongoserrula rarauna* (sic !) DUMITRICĂ – DOSZTÁLY, Pl. 3, Fig. 1

Derivation of name: In honour of Dr. S. GORIČAN, Ljubljana.

Holotype: The specimen on Pl. 13, Fig. 1; rep.-no. KOMO 1994 IV-159

Material: 23 specimens.

Diagnosis: Spongy shell with long, needle-like antapical polar spine and few needle-like by-spines of different length in the lower hemisphere. Polar spine completely flattened, sickle-shaped. Blade widest at the end of the proximal third. Its width decreases slowly and gradually toward the pointed, distal end. Distal part rather strongly recurved. No lobe on the external margin of the proximal blade. The 6–8 denticles are slender, in their distal part needle-shaped, pointed or slender-triangular, saw-tooth shaped. The distal denticles are generally slender subtriangular. The first 2–4 denticles are largest, distally their length decreases. The distances between the denticles are in the proximal portion of the blade nearly equal and somewhat lower in the distal portion of the blade.

Measurements:

Diameter of spongy shell: 131–146 μm

Length of polar spine above the shell surface (without denticles): 132–231 μm

Maximum width of polar spine: 56–92 μm

Length of recurved part of the polar spine: 260–308 μm

Maximum length of denticles: 55–74 μm

Occurrence: Late Longobardian of Hungary and Bosnia-Hercegovina.

Remarks: *Spongoserrula rarauana* DUMITRICĂ, 1982 displays a broader blade with distinct heel-like lobe on the external margin of the proximal blade. The distal end of the denticles are blunt or broadly rounded.

In *Spongoserrula cordeyi* n. sp., the distance between the first two proximal denticles is by far larger than between the following denticles.

Spongoserrula fluegeli n. sp. displays longer spines. Especially the first proximal spine is very long and slightly to strongly convex.

Spongoserrula semicircularis n. sp. displays a semicircular blade, widest in its middle part. The proximal lobe is distinct. The triangular denticles are shorter and at least in the distal part inward-bent from the plane of the blade.

Spongoserrula nuda n. sp.
(Pl. 9, Fig. 7)

Derivation of name: According to the completely missing spines or undulations on the external margin of the polar spine.

Holotype: The specimen on Pl. 9, Fig. 7; rep.-no. KOMO 1994 IV-31

Material: 3 specimens.

Diagnosis: Spongy shell small with slightly spiny surface. Polar spine sickle shaped, completely flat, rather narrow. There is a gradual, but very slow widening from the base to the bend of the polar spine and a likewise gradual, a little faster narrowing toward the needle-shaped distal end. The straight proximal part of the polar spine is rather long, with gradual transition to the curved part. The distal part of the polar spine is short and rather slightly recurved. Therefore the polar spine ends considerably above the level of the shell.

Measurements:

Diameter of spongy shell: 80-87 µm

Length of polar spine above the shell surface: 227–233 µm

Maximum width of polar spine: 53 µm

Length of recurved part of the polar spine: 164–167 µm

Remarks: *Spongoserrula nuda* n. sp. remembers in its shape of the polar spine to *Falcispongus* DU-MITRICA, 1982. However, the entire polar spine is completely flattened to a rather narrow blade, whereas in all *Falcispongus* species the rounded primary spine is always recognizable near the inner side of a blade-like part.

Most similar is *Spongoserrula antiqua* n. sp. that has also a smooth external margin. Like in typical *Spongoserrula*, in *S. antiqua* n. sp. the stem is very short or absent.

Material: 1 specimen.

Diagnosis: Polar spine completely flattened, very broad, blade-like. Stem short, relatively narrow. Heel-like lobe at the proximal external margin of the blade high. Two lobe-like, very broad teeth with blunt ends are present, the proximal one is distally bifurcated into two flattened subcylindrical denticles with blunt ends. There is no distal recurved part of the polar spine, but instead of them three long, needle-like teeth are present, from which the uppermost is obliquely upward directed, whereas the other two teeth are obliquely downward directed.

Measurements:

Length of polar spine above the shell surface (without teeth):

195 µm

Maximum width of polar spine: 167 µm

Length of straight stem above the shell surface: 55 µm

Length of proximal teeth: 39–44 µm

Length of needle-like distal spines: 56–106 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Spongoserrula bifurcata* n. sp. is the only similar species. However, it displays distally two long, obliquely downward-directed spines, one of them (the upper one) corresponds to the needle-like terminal recurved end of the polar spine in other *Spongoserrula* species. In the proximal part of this terminal spine a short outer spine is present, which is obliquely upward directed. If this spine will be prolongated to a long, needle-like spine, then this form would be nearly identical with *S. ornata*. It cannot be excluded that *S. ornata* is a pathological form, because only one specimen is present.

Spongoserrula ornata n. sp.
(Pl. 5, Fig. 1)

Derivation of name: According to the sculpture.

Holotype: The specimen on Pl. 5, Fig. 1; rep. no. KOMO 1994 IV-38

Spongoserrula raridenticulata n. sp
(Pl. 12, Fig. 1)

Derivation of name: According to the low number of denticles, unusual for species with pointed denticles.

Holotype: The specimen on Pl. 12, Fig. 1; rep.-no. KOMO 1994 IV-141

Material: 4 specimens.

Diagnosis: Polar spine completely flattened. Stem very short or absent. Blade relatively narrow, in the proximal half of nearly equal width, distally the width decreases slowly. Proximal lobe on the external margin indistinct. Distal end of the blade with short needle-like terminal spine. The 4 widely spaced denticles are short. Three of them are slender triangular, distally pointed, without distinct size differences. The second or the proximal denticle is somewhat longer than the other two denticles. The distal denticle is very low, broad, rounded, rather a small lobe.

Measurements:
Length of the polar spine above the shell surface (without denticles): 115–123 μm
Maximum width of the polar spine: 54–59 μm
Length of recurved part of the polar spine: 294–312 μm
Maximum length of denticles: 38–54 μm

Occurrence: Very rare in the early late Longobardian *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone at the type locality.

Remarks: All other *Spongoserrula* species of the *S. fluegeli* group with pointed or needle-like spines display a larger number of spines. *Spongoserrula rarauana trinodosa* n. subsp. and *S. bidentata* n. sp. of the *S. rarauana* group display few denticles, but all of them are rounded.

mal stem, which is very short and distinctly narrower than the blade. Distal part of polar spine strongly recurved, nearly parallel to the proximal stem. The distal end of the polar spine is situated about in the level of the central part of the shell. Heel-like lobe on the external margin of the proximal blade distinct, but rather small. The 5-6 denticles at the external margin of the blade are short, triangular, with pointed tips. The first 2 or 3 denticles have about the same length, the distally following denticles decreases in length, but their width at the base remains nearly constant.

Measurements:
Length of polar spine above the shell surface (without denticles): 167–172 μm
Maximum width of polar spine: 50–56 μm
Length of recurved part of the polar spine: 159–190 μm
Maximum length of denticles: 28–33 μm
Maximum length of denticles: 28–39 μm

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: The polar spine of *Spongoserrula rarauana* DUMITRICĂ, 1982 is not semicircular, displays a broader blade and the mostly larger denticles are distally blunt or rounded.

The polar spine of *Spongoserrula goricanae* n. sp. is not semicircular, the denticles are larger and there is no heel-like lobe on the external margin of the proximal blade.

Spongoserrula semicircularis n. sp.
(Pl. 9, Fig. 3)

Derivation of name: According to the semicircular blade-like polar spine.

Holotype: The specimen on Pl. 9, Fig. 3; rep.-no. KOMO 1994 IV-43

Material: 4 specimens.

Diagnosis: Polar spine completely flattened, narrow blade-like, with semicircular outline. The blade is widest in its middle part and decreases slowly and gradual toward the needle-like distal part and very slowly and gradual toward the proxi-

Genus *Paroertlispongus*
KOZUR & MOSTLER, 1981

Type species: *Paroertlispongus multispinosus* KOZUR & MOSTLER, 1981

Paroertlispongus lobatus n. sp.
(Pl. 7, Fig. 11)

Derivation of name: According to the lateral lobe on the polar spine.

Holotype: The specimen on Pl. 7, Fig. 11; rep.-no. KOMO 1994 IV-86

Material: 2 specimens.

Diagnosis: Spongy shell with one large, straight, needle-like polar spine that displays at the end of the proximal third a shallow, but distinct semielliptical lobe.

Measurements:

Diameter of shell: 92–100 μm

Length of polar spine (only in one specimen fully preserved): 280 μm

Width of polar spine in its proximal third: 8 μm

Width of lobate part of the polar spine: 16 μm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: Stratigraphic youngest known species of *Paroertlispongus*. *Paroertlispongus lobatus* n. sp. is distinguished from Anisian and Early Ladinian species of *Paroertlispongus* by the presence of a lobe on the straight, long, needle-like polar spine.

Genus *Bogdanella*
KOLAR-JURKOVŠEK, 1989 emend.

Type species: *Bogdanella trentana* KOLAR-JURKOVŠEK, 1989

Occurrence: Longobardian of southern Tethys.

Remarks: KOLAR-JURKOVŠEK (1989) placed in this genus all oertlipongids with strongly curved spines. Beside the type species with corkscrew-like twisted polar spine, she assigned to this genus also *Oertlispongus* species with strongly, but simply recurved polar spines. *Bogdanella* is herein restricted to species with corkscrew-like apical polar spine. A short, needle-like antapical polar spine is often present, but may be replaced by a bunch of short, needle-like by-spines near the antapical pole.

Bogdanella KOLAR-JURKOVŠEK, 1989 is near related to *Oertlispongus* DUMITRICA, KOZUR & MOSTLER, 1980. Like in this genus, the primitive *Bogdanella precursor* n. sp. from the lower sub-

zone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone displays a long straight, distally slightly curved stem before the corkscrew-like twisted part, whereas this part is very short in the stratigraphically youngest *Bogdanella cordevolica* n. sp. In primitive forms there are two, in advanced forms three distinct turns.

Bogdanella trentana KOLAR-JURKOVŠEK, 1989
(Pl. 7, Figs. 7–9, 12, 13)

1989 *Bogdanella trentana* n. g. n. sp. – KOLAR-JURKOVŠEK, p. 162, Fig. 3, no. 1

Description: Spongy shell with tiny spines and short, needle-like antapical polar spine. Main (apical) polar spine corkscrew-like twisted. The straight proximal part is short and followed by a very slight, partly indistinct turn and two or three large turns. The main polar spine is round to moderately flattened (circular to elliptical cross section).

Occurrence: Common in the *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (late Longobardian) of Slovenia and Bosnia-Hercegovina.

Remarks: In *Bogdanella bosniensis* n. sp. the second large turn is acute and the polar spine is in this level even a little recurved. After this turn the polar spine is rather broad and displays a distinct furrow.

In *Bogdanella cordevolica* n. sp. the straight proximal part is extremely short to nearly missing and also the first turn is very distinct.

Bogdanella trentana balkanica n. subsp.
(Pl. 7, Figs. 7–9, 12, 13)

Derivation of name: According to the common occurrence in the Balkan region.

Holotype: The specimen on Pl. 7, Fig. 7; rep.-no. KOMO 1994 IV-88

Material: More than 100 specimens.

Diagnosis: With the character of the species. Straight stem short, with circular cross section.

First turn very indistinct. The following three large turns are in lateral view visible as large waves. Polar spine in the twisted part moderately flattened, with elliptical cross section.

Measurements:
Diameter of spongy shell: 80–100 µm
Length of polar spine: 275–360 µm
Maximum width of polar spine: 18–25 µm
Length of straight proximal part of polar spine: 35–80 µm
Length of twisted part of polar spine: 225–280 µm
Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: See also under the species.

According to KOLAR-JURKOVŠEK (1989) the cross section of the polar spine is circular. In *Bogdanella trentana balkanica* n. subsp. only the straight short proximal portion of the polar spine displays a circular cross section. The large twisted part of the main polar spine is moderately flattened and displays an elliptical cross section. Moreover, *Bogdanella trentana trentana* KOLAR-JURKOVŠEK, 1989, displays only two big turns.

Bogdanella bosniensis n. sp.
(Pl. 7, Fig. 6)

Derivation of name: According to the occurrence in Bosnia-Hercegovina.
Holotype: The specimen on Pl. 7, Fig. 6; rep.-no. KOMO 1994 IV-87
Material: 4 specimens.
Diagnosis: Polar spine corkscrew-like twisted. In the proximal straight part the cross section of the polar spine is circular, in the very distal part oval, in the remaining parts the polar spine is moderately flattened. In lateral view the first turn of twisting is broadly rounded, the seconds on is acute with a slight backward recurving. The third turn is again broadly rounded. After the second turn the polar spine is rather broad, with a deep median furrow that becomes shallower and finally indistinct towards the distal end.

Measurements:
Length of polar spine: 233–253 µm
Length of straight proximal portion of polar spine: 50–53 µm
Length of twisted portion of polar spine: 183–200 µm
Maximum width of polar spine: 28–30 µm
Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Bogdanella trentana* KOLAR-JURKOVŠEK, 1989 has no acute turn in the polar spine and a median furrow is absent.

Bogdanella cordevolica n. sp.
(Pl. 13, Fig. 12)

Derivation of name: According to the occurrence in the Cordevolian of Sicily.
Holotype: The specimen on Pl. 13, Fig. 12; rep.-no. KOMO 1994 IV-169
Material: 2 specimens.
Diagnosis: Spongy shell with tiny spines. Polar spine not flattened, with circular cross section. Straight proximal portion above the shell very short. All three turns large, in lateral view visible as large waves.
Measurements:
Diameter of spongy shell: 152–158 µm
Length of polar spine: 377–400 µm
Length of straight proximal portion of polar spine: 5–27 µm
Length of twisted portion of polar spine: 372–373 µm
Maximum width of polar spine: 31 µm
Occurrence: Very rare in the Cordevolian of the Sosio Valley area, Sicily.
Remarks: *Bogdanella trentana* KOLAR-JURKOVŠEK, 1989 displays a somewhat longer straight proximal part of the polar spine. The first turn is indistinct and only the following 2-3 turns are strong.

In *Bogdanella bosniensis* n. sp. the first turn is also strong, but the polar spine is broad in the distal half and displays there a median furrow.

Bogdanella praecursor n. sp.
(Pl. 15, figs. 13-15)

1991   *Bogdanella trentana* KOLAR-JURKOVŠEK - DOSZTÁLY, Pl. 1, Fig. 4

Derivation of name: According to the ancestral position to the other known *Bogdanella* species.

Holotype: The specimen on Pl. 15, Fig. 13; rep.-no. KOMO 1994 IV-199

Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).

Type stratum: Middle part of Buchenstein Beds, sample St 1.

Material: 34 specimens.

Diagnosis: Spongy shell with a bunch of needle-like, very short by-spines around the antapical pole. Polar spine cork-screw-like twisted, with long straight proximal part and moderately long twisted part with two large turns, visible in lateral view as large waves. The entire polar spine has a circular cross section or it is slightly flattened around the first turn, where the cross section may be broadly elliptical.

Measurements:

Diameter of spongy shell: 106–142 µm

Length of polar spine: 282–383 µm

Length of straight proximal portion of polar spine: 88–133 µm

Length of twisted portion of polar spine: 188–233 µm

Maximum width of polar spine: 23–33 µm

Occurrence: Common in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality. Rare in the middle Subzone (*Spongoserrula rarauana* Subzone) of *M. cochleata* Zone (middle Longobardian) of Hungary.

Remarks: All other known *Bogdanella* species display a shorter straight part of the polar spine. Moreover, in *Bogdanella trentana balkanica* n. subsp., *B. bosniensis* n. sp. and *B. cordevolica* n. sp. three strong turns are present. In *Bogdanella trentana balkanica* n. subsp. the polar spine is moderately flattened and displays an elliptical cross section except the short straight proximal part with circular cross section. In *Bogdanella bosniensis* n. sp. the distal half of the polar spine is strongly flattened and displays a median furrow.

Genus *Gibberospongus* n. gen.

Type species: *Gibberospongus spinosus* n. gen. n. sp.

Derivation of name: According to the cylindrical or spine-like process.

Diagnosis: The spongy spherical shell displays a differentiated apical polar spine and several small needle-like by spines of irregular distribution. The polar spine is proximally blade-like widened. The original spine is included into the inner side of the blade, but partly not more recognizable. The distal part of the spine is long, needle-like and moderately to strongly recurved. At the distal external end of the blade a spine or a cylindrical appendage is present. Rarely this appendage starts somewhat distally of the blade. A second spine may be present in the proximal part of the blade.

Assigned species:

Gibberospongus spinosus n. gen. n. sp.

Gibberospongus bispinosus n. sp.

Gibberospongus kraineri n. sp.

Gibberospongus tichyi n. sp.

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) of Bosnia-Hercegovina.

Remarks: *Gibberospongus* n. gen. has evolved from *Falcispongus transitus* n. sp. by development of one or two appendages on the blade-like part of the polar spine. It is seemingly restricted to the late Longobardian.

In *Spongoserrula* DUMITRICĂ, 1982 the largest part of the polar spine is blade-like and the external margin displays several denticles or cylindrical appendages.

Gibberospongus spinosus n. gen. n. sp.
(Pl. 8, Fig. 6; Pl. 9, Figs. 6, 9, 11, 12, 16, 18; Pl. 12, Fig. 15)

Derivation of name: According to the spine-like appendage of the blade.

Holotype: The specimen on Pl. 9, Fig. 9; rep.-no. KOMO 1994 IV-12

Material: More than 100 specimens.

Diagnosis: Straight stem of the polar spine short, rarely absent. Blade-like part of the polar spine elongated, rounded subrectangular. It is situated in prolongation of the stem or slightly oblique to it. External margin of the blade straight to slightly convex; inner margin straight to slightly concave. At the outer distal corner of the blade a spine is always present. This spine and the distal corner of the blade may be upward bent (Pl. 9, figs. 6, 11). The polar spine is included into the inner margin of the blade, but sometimes not well separable from the blade. The distal portion of the polar spine is needle-like and strongly recurved. This part of the polar spine is very long.

Measurements:
Length of straight stem of polar spine: 0–20 µm
Length of the blade-like part of the polar spine: 127–150 µm
Maximum width of the blade-like part of the polar spine: 50–75 µm
Length of recurved narrow part of the polar spine: 200–278 µm

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Gibberospongus kraineri* n. sp. displays a cylindrical appendage at the distal outer end of the blade instead of a spine.

Gibberospongus bispinosus n. sp. displays a long, distally broadened, flat stem and an additional spine at the transition between the stem and the blade.

Gibberospongus bispinosus n. sp.
(Pl. 9, Fig. 8)

Derivation of name: According to the presence of two spine-like appendages.
Holotype: The specimen on Pl. 9, Fig. 8; rep.-no. Komo 1994 IV-19
Material: 4 specimens.
Diagnosis: Straight stem of the polar spine long, but only basally roundish. Its distal part is flat and blade-like widened. The blade-like part lies about in the midst of the polar spine. Its transitions to the stem and to the recurved part of the polar spine are gradual. It has a straight external margin and a strongly concave inner margin. At the outer distal end of the blade a spine is present. A second long, slightly recurved spine is situated at the transition between the stem and the blade. It is directed in opposite direction to the distal end of the main spine. The recurved part of the polar spine is relatively short, in its proximal part rather broad and blade-like, flat. It tapers gradually to a needle-like distal part.

Measurements:
Length of straight stem of polar spine: 108 119 µm
Length of the blade-like part of the polar spine: 112–120 µm
Maximum width of the blade-like part of the polar spine: 69–73 µm
Length of recurved part of the polar spine: 155–167 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Gibberospongus bispinosus* n. sp. is clearly distinguished from all other *Gibberospongus* species by the form of the polar spine with two spines at the ends of the blade. Except the base of the stem and the distal end, the polar spine is blade-like without separation of spine and blade. By this character, *Gibberospongus bispinosus* is similar to *Spongoserrula* DUMITRICĂ, 1982. However, the spine at the distal outer end of the blade lies exactly in the same position as in the other *Gibberospongus* species.

In *Gibberospongus* cf. *bispinosus* that is probably a pathological form (only one specimen is present), the spine one the distal end of the blade is recurved and its distal end joins the proximal part of the terminal spine of the blade, where a further spine is situated.

Gibberospongus kraineri n. sp.
(Pl. 8, Figs. 1; Pl. 9, Fig. 17)

Derivation of name: In honour of Doz. Dr. K. KRAINER, Innsbruck.

Holotype: The specimen on Pl. 9, Fig. 17; rep.-no. KOMO 1994 IV-2

Material: 23 specimens.

Diagnosis: The globular spongy shell displays one polar spine and several short, irregularly distributed needle-like by-spines. The polar spine widens immediately above the shell surface to a rounded, elongated subrectangular blade which is situated obliquely to the polar axis. The blade has a straight or convex outer, and a concave inner margin. At the outer part of the distal end of the blade a short cylindrical appendage is present. The spine is included into the inner margin of the blade. Its long recurved part is narrow and ends parallel to the centre of the shell.

Measurements:

Diameter of shell: 104–120 µm

Length of straight stem: 0–15 µm

Length of blade-like part of the polar spine: 95–117 µm

Maximum width of blade-like part of the polar spine: 53–61 µm

Length of recurved narrow part of the polar spine: 200–250 µm

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: In *Gibberospongus tichyi* n. sp. the round, but rather narrow appendage does not branch off from the end of the blade, but from the basal part of the recurved spine.

In *Gibberospongus spinosus* n. sp. and in *G. bispinosus* n. sp. the appendages are spines.

Gibberospongus kraineri n. sp. is a transitional form between typical *Gibberospongus* with 1–2 spine-like appendages at the outer distal corner of the blade-like part of the polar spine, and *Falcispongus* without such appendages. Close relations exists to *Falcispongus transitus* n. sp., the ancestral form of *Gibberospongus*. In this species, there is a round distal widening of blade, but not yet an appendage. Rare transition forms between both species are present (*Falcispongus* cf. *transitus* n. sp., Pl. 8, Fig. 2). In these forms the distal expansion of the blade is almost as long as the cylindrical appendage of *Gibberospongus kraineri* n.sp., but

it is not yet separated from the blade to form an appendage at the outer distal corner.

Gibberospongus tichyi n. sp.
(Pl. 9, Fig. 2)

Derivation of name: In honour of Prof. Dr. G. TICHY, Salzburg.

Holotype: The specimen on Pl. 9, Fig. 2; rep.-no. KOMO 1994 IV-20

Material: 3 specimens.

Diagnosis: Straight stem of the polar spine short. Blade wing-like, not much separated from the spine. Recurved part of the polar spine long, needle-shaped. On its basal part a perpendicular, cylindrical appendix is present.

Measurements:

Length of straight stem of polar spine: 11–17 µm

Length of blade-like part of the polar spine: 105–117 µm

Maximum width of blade-like part of the polar spine: 52–58 µm

Length of recurved part of the polar spine: 306–333 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Gibberospongus tichyi* n. sp., is distinguished from all other *Gibberospongus* species by the position of the cylindrical appendage at the base of the recurved part of the polar spine and not at the outer distal end of the blade.

Genus *Scutispongus* n. gen.

Type species: *Scutispongus tortilispinus* n. gen. n. sp.

Derivation of name: According to the shield-like blade of the polar spine.

Diagnosis: Spongy shell with few to numerous needle-like by-spines in the antapical hemisphere. A small needle-like antapical polar spine may be

present, but it is not distinctly larger than the by-spines. The main (apical) polar spine is very large. Straight stem always present, mostly long, partly broad, a little to completely flattened. Blade large, completely flattened, but in prolongation of the stem the primary polar spine may be still visible as an axial swelling. The blade is bilateral, mostly symmetrical, partly asymmetrical, rarely strongly asymmetrical. Its wings terminate on both sides in a needle-like spine. Only in the most primitive form, transitional to *Falcispongus* DUMITRICĂ, 1982, on one side the wing lacks a terminal spine. A partly twisted apical spine of different length is often present opposite to the stem. It may be cylindrical or completely flattened. External margin generally without denticles, but often with slight to strong undulations or lateral incisions. Long, needle-like denticles may be present only in very few aberrant forms.

Assigned species:

Scutispongus tortilispinus n. gen. n. sp.
Falcispongus rostratus DUMITRICĂ, 1982
Pterospongus rostratus rostratus (DUMITRICĂ, 1982)
Pterospongus rostratus incurvatus n. subsp.
Pterospongus rostratus parvispinus n. subsp
Pterospongus undulatus DUMITRICĂ, 1982
Pterospongus bogdani KOLAR-JURKOVŠEK, 1989
Scutispongus bogdani bogdani (KOLAR-JURKOV-ŠEK, 1989)
Scutispongus bogdani ancoraeformis n. subsp.
Pterospongus aquilus DOSZTÁLY, 1991 nom. corr.
Scutispongus alienus n. sp.
Scutispongus baloghi n. sp.
Scutispongus bicornutus n. sp.
Scutispongus bituberosus n. sp.
Scutispongus cephalus n. sp.
Scutispongus dumitricai n. sp.
Scutispongus gackoensis n. sp.
Scutispongus? *gracilispinosus* n. sp.
Scutispongus latus n. sp.
Scutispongus? *parvifoliatus* n. sp.
Scutispongus? *parvifoliatus parvifoliatus* n. subsp.
Scutispongus? *parvifoliatus postera* n. subsp.
Scutispongus ploechingeri n. sp.
Scutispongus ploechingeri ploechingeri n. subsp.

Scutispongus ploechingeri lobatus n. subsp.
Scutispongus reschi n. sp.
Scutispongus sagittaeformis n. sp.
Scutispongus semifusus n. sp.

Occurrence: One of the most characteristic radiolarian genera of the Tethyan Longobardian, but still present in the Cordevolian.

Remarks: Within *Scutispongus* n. gen. two species groups can be observed. In one group, an apical spine of different shape and size is present and the external margin is distinctly undulated. The type species belongs to this group. In the other group, the external margin of the blade is smooth or slightly undulated. *Scutispongus bogdani* (KOLAR-JURKOVŠEK, 1989) is a typical representative of this latter group. There are all transitions between these two groups. Transition forms display mostly an undulation on one side and the apical end is pointed or displays a node-like apical prolongation as equivalent of the apical spine.

Pterospongus DUMITRICĂ, 1982 displays a distinct apical incision opposite to the stem. This genus is restricted to the lower and middle *Muelleritortis cochleata* Zone. The smooth forms are morphologically similar to *Scutispongus*, but the presence of an incision opposite to the stem is a good distinctive feature. All transition forms between smooth *Pterospongus* DUMITRICĂ, 1982 and *Baumgartneria* DUMITRICĂ, 1982 of the *B. curvispina* group are known. On the contrary, *Scutispongus* evolved from *Falcispongus* DUMITRICĂ, 1982 (see below). The ancestors of the spined *Pterospongus* (type species *Pterospongus patrulii* DUMITRICĂ, 1982) are not known yet. They probably evolved from *Baumgartneria dumitricae* DOSZTÁLY, 1991, by developing a wider blade and more spines. In this case *Pterospongus* would be a natural unit, morphologically connected by the incision opposite to the stem. However, at the present stage of our knowledge, direct relations of the spined (type) *Pterospongus* to *Steigerispongus* n. gen. cannot be excluded, from which they are distinguished by the apical incision opposite to the stem. The stratigraphic succession of the forms favours the above mentioned close relations between the smooth and spined *Pterospongus* as originally assumed by DUMITRICĂ (1982).

Scutispongus n. gen. has evolved from *Falcispongus* DUMITRICA, 1982, to which a part of *Scutispongus* was placed by DUMITRICĂ (1982). The transitional form is *Scutispongus rostratus* (DUMITRICĂ, 1982). This species displays already a bilateral, but still strongly asymmetric shield-like blade. Only on one side a spined wing is present. The wing on the other side has no terminal spine. *Scutispongus rostratus* is therefore different from *Falcispongus*, in which only unilateral an unilateral polar spine is present. It is closer related to *Scutispongus*, but distinguished from typical *Scutispongus* by the asymmetric blade (rarely present in typical *Scutispongus*) and above all by the missing terminal spine at one of the wings. *S. rostratus* begins stratigraphically before the first typical *Scutispongus* species that are bilateral symmetric and display spined wings on both sides.

Scutispongus tortilispinus n. gen. n. sp.
(Pl. 1, Figs. 7, 9–11; Pl. 8, Figs. 7, 8

Derivation of name: According to the twisted, flattened apical spine.
Holotype: The specimen on Pl. 1, Fig. 11; rep.-no. KOMO 1994 IV-93
Material: More than 100 specimens.
Diagnosis: Spongy shell with numerous needle-like by-spines in the lower hemisphere. Around the antapical pole, these by-spines are moderately long, the remaining ones are short. Apical polar spine completely flattened, with shield-like, large, broad blade, which has two distinct, rather deep incisions above the wings. Blade above the incision distinctly larger than blade of the wings below the incision. Immediately below the incisions, on the proximal part of the wing, broad undulations or shallow nodes are present. Immediately above the incision an undulation or shallow node may be also present. Apical spine completely flattened, twisted, mostly with bifurcated or modified bifurcated apical end. Rarely the end of the apical spine is round or blunt. Often it is blunt with two short spines at the corners (modified bifurcated). The twisted margins of the flattened apical

spine are connected with the external margin of the blade which is in the apical half of the blade upturned in the direction of the twisting (in opposite direction on the two sides of the blade). The wings end in moderately long, needle-like spines that are obliquely backward directed. Stem short to moderately long, in the upper part distinctly widened.
Measurements:
Diameter of shell: 100–110 µm
Length of polar spine above the shell surface (without apical spine): 200–220 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 109–146 µm
Length of straight stem above the shell: 60–88 µm
Width of straight stem in its middle part: 29–36 µm
Length of terminal spines of the wings: 105–167 µm
Length of apical spine: 20–47 µm
Occurrence: Very common in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Scutispongus undulatus* (DUMITRICĂ, 1982) displays a strongly and regularly undulated surface of the blade. The apical spine is cylindrical and represent the continuation of an axial cylindrical or flattened cylindrical elevation within the blade and stem.

Scutispongus latus n. sp. displays a flattened triangular, apically pointed spine that is not or only slightly twisted.

Scutispongus longispinosus n. sp. displays a very long, needle-like apical spine. The lateral incisions are situated somewhat above the midst of the blade. Therefore the upper part of the blade is smaller than the blade of the wings.

Scutispongus rostratus (DUMITRICĂ, 1982)
(Pl. 15, Figs. 6-10, 12)

1982 *Falciformis* (sic!) *rostratus* n. sp., pars – DUMITRICĂ, p., 66, Pl. 3, Figs. 8, 9; Pl. 4, Figs. 2, 3 (?), 5, 6 (?); Pl. 5, Figs. 2 (?), 4 (?)
1982 *Falcispongus* sp. 1 – DUMITRICĂ, p. 67, Pl. 33, Fig. 7

1990 *Falcispongus rostratus* DUMITRICĂ, 1982 a
      - GORIČAN & BUSER, p. 145, Pl. 3, Fig. 12
1991 *Falcispongus rostratus* DUMITRICĂ – DOSZ-
      TÁLY, Pl. 1, Fig. 1

Material: More than 100 specimens.

Description: Spongy shell with several needle-like by-spines in the lower hemisphere. One of these by-spines is generally situated in the position of an antapical polar spine, but it is not larger than the other by-spines. Stem moderately long. Blade large, bilateral, but strongly asymmetric. At one side (primary blade), the wing ends rather invariably in a needle-like terminal spine that is obliquely backward directed, rarely strongly curved out of the blade's plane. At the other side (secondary blade) the wing is either rounded triangular with rounded end or blunt. In the latter case often a lobe with round, rarely blunt end is present. Between all these morphotypes transition forms are present during the entire stratigraphic range of the species. Rarely, the lobe may have a tiny terminal spine.

Occurrence: Early Longobardian *Budurovigna-thus hungaricus* conodont zone to middle subzone (*Spongoserrula rarauana* Subzone) of *Muelleri-tortis cochleata* Zone (middle Longobardian). Common in the lower subzone (*Pterospongus priscus* Subzone) of *M. cochleata* Zone (early middle Longobardian). Romania, Slowenia, Hungary, Bosnia-Hercegovina.

  S. rostratus (DUMITRICĂ, 1982) begins according to DUMITRICĂ (1982) in the lower Fassanian. However, from all his assumed Fassanian samples, *S. rostratus* was only reported from sample 78/1. In our material, *S. rostratus* is not present before the Longobardian and in our rich early and middle Fassanian samples with several thousands oertlispongids, *S. rostratus* is never present. In our late Fassanian material this species was not found as well, but from this stratigraphic level we have only a few thousands radiolarians with only about 100 oertlispongids.

Remarks: *Scutispongus rostratus* (DUMITRICĂ, 1982) is a transition form between *Falcispongus* DUMITRICĂ, 1982 and *Scutispongus* n. gen. Like in all *Scutispongus* species, the blade is bilateral. However, the blade is strongly asymmetric, whereas most of *Scutispongus* species are bilateral symmetric or nearly symmetric. Exceptionally, also the blade of typical *Scutispongus* is strongly asymmetrical (*S. dumitricai* n. sp., *S. parvifoliatus* n. sp. and *S. reschi* n. sp.). In typical *Scutispongus*, also in forms with strongly asymmetric blade, both wings ends in needle-like spines. In *Scutispongus rostratus*, however, only at one side (primary blade) the wing ends in a needle-like terminal spines. At the other side, the wing ends rounded triangular, blunt or lobe-like with rounded end. In *Scutispongus rostratus minutispinus* n. subsp. a tiny spine is present at the end of the lobe. This form is a transition form to advanced *Scutispongus*.

Scutispongus rostratus rostratus (DUMITRICĂ, 1982)
(Pl. 15, Figs. 6, 7, 10, 12)

1982 *Falciformis* (sic!) *rostratus* n. sp., pars –
      DUMITRICĂ, p., 66, Pl. 3, Figs. 8, 9; Pl. 4,
      Figs. 2, 3(?), 5, 6 (?); Pl. 5, Figs. 2 (?), 4 (?)
1990 *Falcispongus rostratus* DUMITRICĂ, 1982 a
      – GORIČAN & BUSER, p. 145, Pl. 3, Fig. 12
1991 *Falcispongus rostratus* DUMITRICĂ – DOSZ-
      TÁLY, Pl. 1, Fig. 1

Material: More than 100 specimens.

Description: With the character of the species. Terminal spine of primary blade situated in the plane of blade and backward directed. Secondary blade without terminal spine, but otherwise variable in shape and size. The secondary blade is mostly triangular with rounded distal end. It may be also blunt or oblique, mostly with a lobe in the lower portion that ends roundish, rarely blunt. This lobe may gradually develop from the secondary blade or it is distinctly separated. Between all these different morphotypes transitions are present throughout the stratigraphic range of the subspecies.

Measurements:
Diameter of spongy shell: 120–127 μm
Length of polar spine above the shell surface: 219–237 μm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 127–140 µm

Length of straight stem above the shell: 80–100 µm

Width of straight stem in its middle part: 27–33 µm

Length of the terminal spine of the primary blade: 80–147 µm

Occurrence: Common in the lower and middle Longobardian. Peak occurrence in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian). So far only known from the European Tethys.

Remarks: See also under the species.

In *Scutispongus rostratus incurvatus* n. subsp. the terminal spine of the primary blade is strongly curved out the blade's plane.

In *Scutispongus rostratus minutispinus* n. subsp. the rather long lobe bears a tiny terminal spine.

Scutispongus rostratus incurvatus n. subsp.
(Pl. 15, Fig. 8)

Derivation of name: According to the terminal spine of the primary blade that is strongly curved out of the blade's plane.

Holotype: The specimen on Pl. 15, Fig. 8; rep.-no. KOMO 1994 IV-196

Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).

Type stratum: Middle part of Buchenstein Beds, sample St 1.

Material: 2 specimens.

Diagnosis: With the character of the species. Terminal spine of primary blade strongly curved out of the blade's plane. Secondary blade large, rounded triangular.

Measurements:

Length of polar spine above the shell surface: 164–170 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 103–107 µm

Length of straight stem above the shell: 55–61 µm

Width of straight stem in its middle part: 23 µm

Occurrence: Very rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: See also under the species.

The terminal spine of the primary blade of *Scutispongus rostratus rostratus* (DUMITRICĂ, 1982) lies in the plane of the blade.

Scutispongus rostratus minutispinus n. sp.
(Pl. 15, Fig. 9)

1982 *Falcispongus* sp. 1 – DUMITRICĂ, p. 67, Pl. 33, Fig. 7

Derivation of name: According to the tiny terminal spine on the lobe.

Holotype: The specimen on Pl. 15, Fig. 9; rep.-no. KOMO 1994 IV-197

Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).

Type stratum: Middle part of Buchenstein Beds, sample St 1.

Material: One specimen.

Diagnosis: With the character of the species. Blade strongly asymmetric. Primary curved spine well visible within the blade. Inner part of the blade narrow, outer part wide as typical for *S. rostratus*. Lobe long, obliquely backward directed, with blunt end that bears at the inner side a tiny terminal spine. The lobe is distinctly separated from the blade that has a vertical external margin above the lobe.

Measurements:

Diameter of spongy shell: 120–127 µm

Length of polar spine above the shell surface: 247 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 141 µm

Length of straight stem above the shell: 93 µm

Width of straight stem in its middle part: 30 µm

Length of terminal spine of the primary blade: 100 µm

Length of lobe: 100 µm

Length of terminal spine on the lobe: 20 μm

Occurrence: Very rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: DUMITRICĂ (1982) figured a broken specimen which occur together with *Scutispongus rostratus* (DUMITRICĂ, 1982). He stated that this form belongs „undoubtedly to a different species." Our well preserved specimen can be rather regarded as subspecies of *Scutispongus rostratus* (DUMITRICĂ, 1982), but we cannot exclude that DUMITRICĂ (1982) was right in regarding this form as a independent species.

Scutispongus rostratus rostratus (DUMITRICĂ, 1982) has no terminal spine on the lobe that is terminally rounded.

Scutispongus rostratus minutispinus n. subsp. is a transition form from *S. rostratus* to advanced *Scutispongus* that have a terminal spine on both wings of the blade.

Scutispongus undulatus (DUMITRICĂ, 1982)
(Pl. 1, Figs. 4–6)

1982 *Pterospongus undulatus* n. sp. – DUMITRICĂ, p. 69, Pl. 6, Fig. 6; Pl. 7, Figs. 1–3

Description: Polar spine flattened, spear-shaped, with axial cylindrical or slightly flattened cylindrical part that is prolongated in a cylindrical apical spine ending in a short, needle-like tip. External margin of the blade with 2–3 lobes. The wings end in short to moderately long, needle-like, obliquely backward directed spines. Stem moderately long, in its upper part considerably widened.

Occurrence: Common in the middle and late Longobardian of Romania, Hungary and Bosnia-Hercegovina. According to DUMITRICĂ (1982) this species was derived from the Cordevolian sample R 88. The Cordevolian age was determined by radiolarians. However, this sample has a typical oertlispongid fauna of the middle *Muelleritortis cochleata* Zone with *Falcispongus ? rostratus* DUMITRICĂ, *Spongoserrula*

rarauana DUMITRICĂ (typical specimens with rounded spines) and *Scutispongus undulatus* (DUMITRICĂ). In our material, this species is not present in the Cordevolian, but rare in the middle Longobardian and common in the late Longobardian.

Remarks: Already DUMITRICĂ (1982) stated that this species is not near related to the other *Pterospongus* species. It fits well into the new genus *Scutispongus*, but can be easily separated from the other *Scutispongus* species by the cylindrical apical spine in continuation of a cylindrical or slightly flattened cylindrical axial part within the otherwise completely flattened blade.

Scutispongus bogdani
(KOLAR-JURKOVŠEK, 1989)
(Pl. 3, figs. 13, 5, 10;
Pl. 4, Figs. 2, 4, 9; Pl. 8, Fig. 9)

1982 *Falcispongus* sp. 2 – DUMITRICĂ, p. 67, Pl. 4, Fig. 4
1989 *Pterospongus bogdani* n. sp. – KOLAR-JURKOVŠEK, p. 160–161, Fig. 3, no. 3

Description: Spongy shell in the lower hemisphere with several short, small, needle-like by-spines or with 1–2, long, needle-like spines near the antapical pole. Stem short or long. Blade subhemicircular to subhemielliptical. External margin smooth, rarely at the base of the wings with indistinct, shallow incision. Terminal spines of wings needle-like, moderately long to long, rarely rather short, obliquely backward directed.

Measurements: See under the subspecies.

Occurrence: Very common in the late Longobardian of Slowenia, Hungary, and Bosnia-Hercegovina.

Remarks: The type material is badly preserved. Therefore by-spines are not preserved.

DUMITRICĂ (1982) assigned a typical specimen of *Scutispongus bogdani* (KOLAR-JURKOVŠEK) to *Falcispongus* sp. 2. However, the bilateral symmetrical or nearly symmetrical shield-like blade with two wings ending in long needle-like termi-

nal spines excludes this form from *Falcispongus* DUMITRICĂ, 1982.

KOLAR-JURKOVŠEK (1989) assigned *Scutispongus bogdani* (KOLAR-JURKOVŠEK, 1989) to *Pterospongus* DUMITRICĂ (1982). However, all *Pterospongus* species display a distinct apical incision opposite to the stem and the type species displays additionally a distinct denticulation of the external margin.

Scutispongus ploechingeri n. sp. displays a subtriangular shield with distinct undulation at least on one side of the shield. *Scutispongus* cf. *bogdani bogdani* (KOLAR-JURKOVŠEK) displays a rounded subtriangular shield with slight undulations on both sides. It is a transition form between *S. bogdani* and *S. ploechingeri*.

Scutispongus baloghi n. sp. displays a node-like, rounded triangular prolongation at he apical end. The distal part of the backward directed terminal spines of the wings are inward curved and join the shell, partly also the stem or they ends immediately beside the shell.

Most similar is *Scutispongus semifusus* n. sp., but in this species the shield is subtriangular and one of the terminal wing spines join the shell.

Two subspecies can be discriminated.

Scutispongus bogdani bogdani (KOLAR-JURKOVŠEK, 1989)
(Pl. 3, Figs. 1, 2, 5, 6; Pl. 4, Fig. 2)

1982 *Falcispongus* sp. 2 – DUMITRICĂ, p. 67, Pl. 4, Fig. 4
1989 *Pterospongus bogdani* n. sp. – KOLAR-JURKOVŠEK, p. 160–161, Fig. 3, no. 3

Holotype: = holotype of the species.
Material: More than 100 specimens.
Diagnosis: With the character of the species. Stem short. Spongy shell with several small, needle-like by-spines near in the lower hemisphere.
Measurements:
Diameter of spongy shell: 100–111 µm
Length of polar spine above the shell surface: 167–222 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 111–161 µm
Length of straight stem above the shell: 56–77 µm
Width of straight stem in its middle part: 25–28 µm
Length of terminal spines of the wings: 106–200 µm
Occurrence: Very common in the late Longobardian of the Tethys.
Remarks: See also under the species.

Scutispongus bogdani ancoraeformis n. subsp. is distinguished by a longer stem. Moreover, the spongy shell is rather small and displays 1–2 long, needle-like spines situated near the antapical pole.

Scutispongus bogdani ancoraeformis n. subsp.
(Pl. 3, Figs. 3, 10; Pl. 4, Figs. 4, 9)

Derivation of name: According to the anchor-shaped polar spine.
Holotype: The specimen on Pl. 4, Fig. 9; rep.-no. KOMO 1994 IV-109
Material: More than 50 specimens.
Diagnosis: With the character of the species. Spongy shell with 1–2 long needle-like by-spines near the antapical pole. Stem of the polar spine long. Blade narrow to moderately wide, external margin with 1–2 slight undulations.
Measurements:
Diameter of shell: 83–106 µm
Length of polar spine above the shell surface: 170–207 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 83–100 µm
Length of straight stem above the shell: 100–117 µm
Width of straight stem in its middle part: 20–23 µm
Length of terminal spines of the wings: 65–105 µm
Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Scutispongus bogdani bogdani* (KOLAR-JURKOVŠEK, 1989) has a shorter stem, the shield-like blade is in average higher, weak undulations are only exceptionally present.

It cannot be excluded that *Scutispongus alienus* n. sp. is a pathological form. However, also according to the form of the apical spine it is different from other known *Scutispongus* species.

Scutispongus alienus n. sp.
(Pl. 7, Fig. 3)

Derivation of name: According to the presence of lateral spines on the blade, unusual for *Scutispongus*.
Holotype: The specimen on Pl. 7, Fig. 3; rep.-no. KOMO 1994 IV-116
Material: One specimen.
Diagnosis: Polar spine completely flattened. Stem long. Blade large, subtriangular, with a deep incision on both sides. At one side below and above the incision two needle-like, very large spines are present. They are laterally curved and reach until the opposite margin of the blade (lower spine) and somewhat beyond this margin (upper spine) respectively. Apical horn pointed, slightly twisted. Terminal spines of the wings needle-like, long.
Measurements:
Length of polar spine above the shell surface (without apical spine): 250 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 144 μm
Length of straight stem above the shell: 100 μm
Width of straight stem in its middle part: 28 μm
Length of terminal spines of the wings: 139 μm
Length of apical spine: 22 μm
Occurrence: One specimen in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Scutispongus latus* n. sp. displays a triangular apical spine and no other spines on the external margin of the blade.

Scutispongus longispinosus n. sp. displays a very long needle-like apical spine and no spines on the external margin of the blade.

Scutispongus baloghi n. sp.
(Pl. 4, Figs. 5, 10)

Derivation of name: In honour of Dr. Z. BALOGH, Innsbruck, who prepared the SEM photos of this paper.
Holotype: The specimen on Pl. 4, Fig. 5; rep.-no. KOMO 1994 IV-114
Material: 4 specimens.
Diagnosis: Spongy shell slightly spiny, by-spines not preserved. Stem moderately long to long. Blade narrow to high, with rounded triangular, node-like apical prolongation and at least at one side with distinct apical shoulder that may be slightly elevated. Terminal spines of the wings long, strongly backward and distally somewhat inward curved. Their ends join the upper part of the shell or the lower part of the stem or ends a little outside the shell surface.
Measurements:
Diameter of shell: 86–91 μm
Length of polar spine above the shell surface (without apical spine): 159–200 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 64–118 μm
Length of straight stem above the shell: 82–105 μm
Width of straight stem in its middle part: 18–29 μm
Length of terminal spines of the wings: 118–159 μm
Length of apical prolongation: 18–29 μm
Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: In *Scutispongus semifusus* n. sp. only one terminal spine of the two wings join the upper shell or basal stem, whereas the other one is obliquely backward directed and ends far away from the shell.

Scutispongus bicornutus n. sp.
(Pl. 12, Fig. 12)

Derivation of name: According to the two short horns at the ends of the strongly inward-curved apical part of the blade.

Holotype: The specimen on Pl. 12, Fig. 12; rep.-no. KOMO 1994 IV-152

Material: 2 specimens.

Diagnosis: Polar spine completely flattened. Only the basal part of the stem is not or only slightly flattened. Stem relatively short, proximally narrow, distally rapidly widening. Blade large, asymmetrical. On one side a long, needle-like terminal spine of the wing is present. On the other side the wing ends in a rounded triangular, backward directed lobe. Apical portion of the blade strongly inward bent. At the ends of this inward bent portion two short apical horns are present.

Measurements:
Length of polar spine above the shell surface (without apical horns): 231–254 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 138–154 µm

Length of straight stem above the shell: 92–100 µm
Width of straight stem in its middle part: 42-46 µm
Length of terminal spine of spined wing: 215–154 µm
Length of apical horns: 9-23 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: The apical incision is a "pseudoincision", caused by the inward bent of the apical portion of the blade. It has nothing to do with the real apical incision of then *Pterospongus* blade.

Most similar is *Scutispongus rostratus* DUMITRICĂ, 1982. However, in this stratigraphically older species the apical part is not inward bent and apical horns are absent.

Holotype: The specimen on Pl. 11, Fig. 9; rep.-no. KOMO 1994 IV-117

Material: 2 specimens.

Diagnosis: Spongy shell with few small, needle-like by-spines, one of them in position of an antapical polar spine. Polar spine completely flattened, except the stem, that is cylindrical in its lower part and marginally flattened in its upper part. Blade of polar spine completely flattened, rather low, with two distinct shoulders that bears shallow, triangular node-like swellings. The central part of the blade displays a shallow, semielliptical elevation. Terminal spines of the wings needle-like, long, obliquely backward directed.

Measurements:
Diameter of shell: 123–131 µm
Length of polar spine above the shell surface: 204–208 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 77–92 µm

Length of straight stem above the shell: 115 µm
Width of straight stem in its middle part: 27–29 µm
Length of terminal spines of the wings: 138–177 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: There are 4 species with shoulders in *Scutispongus*, *S. aquilus* (DOSZTÁLY, 1991), *S. baloghi* n. sp., *S. bituberosus* n. sp. and *S. cephalus*. *S. aquilus* displays a long, laterally bent apical spine and a rather short stem. *S. baloghi* displays a short, rounded triangular apical denticle and the terminal spines of the wings are backward and distally inward curved to join the shell or the basal part of the stem. Near related to *S. bituberosus* is seemingly *S. cephalus*. In this species the shallow, semielliptical blade above the shoulder is strongly enlarged to a large, mushroom-like blade.

Scutispongus bituberosus n. sp.
(Pl. 11, Fig. 9)

Derivation of name: According to the two nodes on the shoulder.

Scutispongus cephalus n. sp.
(Pl. 11, Fig. 13; Pl. 12, Fig. 9)

Derivation of name: According to the head-like shape of the blade above the deep incisions.

Holotype: The specimen on Pl. 12, Fig. 9; rep.-no. Komo 1994 IV-119

Material: 4 specimens.

Diagnosis: Polar spine flattened and blade-like, but in the stem an eccentric, axial, subcylindrical swelling may be present. The wings are narrow, with a distinct shoulder on one or both sides that bear a terminal shallow swelling. Terminal spine of wings large, strongly backward curved, needle-like. Its distal part lies parallel to the stem. On both sides a deep incision is present above the wings. The blade above the wings is inflated mushroom-shaped.

Measurements:

Length of polar spine above the shell surface: 233–242 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 127–162 µm

Length of straight stem above the shell: 110–131 µm

Width of straight stem in its middle part: 33-38 µm

Length of terminal spines of the wings: 140–192 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: Near related to *Scutispongus bituberosus* n. sp., that is distinguished by the small, shallow, semielliptical blade above the shoulders.

Scutispongus dumitricai n. sp.
(Pl. 4, Figs. 11)

Derivation of name: In honour of Dr. P. Dumitrică, Bern

Holotype: The specimen on Pl. 4, Fig. 11; rep.-no. Komo 1994 IV-120

Material: 3 specimens.

Diagnosis: Spongy shell slightly spiny, with few very short by-spines in the lower hemisphere. Polar spine completely flattened, with moderately long stem and bilateral, asymmetric blade. One wing of the blade begins considerably higher at the stem than the other wing. The terminal spine of the wings is at one side long and strongly backward curved, on the other side relatively short and

obliquely backward directed. Above one wing, there is a deep incision and the proximal end of this wing has a shoulder. On the other side no incision is present. The main blade lies opposite to the stem and is also asymmetric.

Measurements:

Diameter of shell: 89-94 µm

Length of polar spine above the shell surface: 178–183 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 107–111 µm

Length of straight stem above the shell: 78–89 µm

Width of straight stem in its middle part: 22 µm

Length of terminal spines of the wings: 83–111 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Scutispongus reschi* n. sp. is distinguished by the presence of an apical spine and by different shape of the blade.

Scutispongus gackoensis n. sp.
(Pl. 12, Fig. 7)

Derivation of name: According to the occurrence in the Gacko area, Bosnia-Hercegovina.

Holotype: The specimen on Pl. 12, Fig. 7; rep.-no. Komo 1994 IV-147

Material: 3 specimens.

Diagnosis: Polar spine completely flattened. Stem relatively short, in the upper part very broad with gradual transition into the moderately large blade. External side of the blade at one or both sides with a shallow lobe. Apical spine broad, triangular, lobe-like with gradual transition to the blade. Terminal spine of the wings moderately long, needle-like, obliquely backward directed.

Measurements:

Length of polar spine above the shell surface: 221–227 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 128–138 µm

Length of straight stem above the shell: 80–87 µm

Width of straight stem in its middle part: 63–67 µm
Length of terminal spines of the wings: 93–113 µm
Length of apical spine: 33–37 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Scutispongus latus* n. sp. displays a narrower stem, the apical spine is narrower and distinctly separated from the blade that displays at one or (mostly) at both sides a deep incision and large lobes.

Scutispongus ploechingeri n. sp. displays a rather indistinct apical lobe instead of an apical spine. The stem is much narrower than in *S. gackoensis*.

Scutispongus baloghi n. sp. displays a similar lobe-like apical spine and a similar blade, but the terminal spines of the wings are strongly backward and inward curved and join at least at one side the spongy shell or the basal part of the stem.

Scutispongus ? gracilispinosus n. sp.
(Pl. 7, Fig. 2; Pl. 12, Fig. 11)

Derivation of name: According to the delicate, needle- like apical spines.
Holotype: The specimen on Pl. 7, Fig. 2; rep.-no. Komo 1994 IV-115
Material: 3 specimens.
Diagnosis: Polar spine completely flattened. Stem moderately long, rapidly widening in its upper part. Blade large, with shallow to deep lateral incision at one or both sides. Two laterally curved, needle-like, long apical spines are situated opposite to the stem in a short distance from each other. Between these two apical spines the blade may be slightly incised. A third needle-like, sideward-directed spine may be present or in this position the shell is inward curved.
Measurements:
Length of polar spine above the shell surface (without apical spine): 178–262 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 100–154 µm

Length of straight stem above the shell: 89–95 µm
Width of straight stem in its middle part: 27–30 µm
Length of terminal spines of the wings: 139–165 µm
Length of apical spines: 78–131 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: 3 specimens with similar, laterally curved, needle-like apical spines are present. For this reason, it is not a pathological form. In the holotype one of the terminal spines of the wings is partly disintegrated into two needle-like spines. This is a pathological feature.

Scutispongus latus n. sp.
(Pl. 1, Figs. 1–3; Pl. 11, Fig. 12)

Derivation of name: According to the broad blade.
Holotype: The specimen on Pl. 1, Fig. 1; rep.-no. Komo 1994 IV-123
Material: More than 100 specimens.
Diagnosis: Surface of spongy shell spiny, with several rather long, needle-like by-spines in the lower hemisphere. One of them lies in the position of an antapical polar spine, but is not larger than the other by-spines. Apical polar spine completely flattened. Stem relatively short. Blade large and wide, with a distinct, rarely indistinct incision above the wings. Apical spine triangular, pointed, sometimes insignificantly twisted. Terminal spines of wings needle-like, mostly moderately long, obliquely backward-directed.
Measurements:
Diameter of shell: 83–87 µm
Length of polar spine above the shell surface (without apical spine): 195–260 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 119–170 µm
Length of straight stem above the shell: 75–100 µm
Width of straight stem in its middle part: 20–31 µm
Length of terminal spines of the wings: 90–130 µm
Length of apical spine: 35–62 µm

Occurrence: Very common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: In *Scutispongus latus* n. sp. the number of pathological forms is rather high (about 1–2 per 100 specimens). Especially frequent is the splitting of spines or spine-like parts of the completely flattened polar spine in 2–3 needle-like spines. In *Scutispongus* cf. *latus* n. sp. (Pl. 4, Fig. 3) a very narrow, needle-like spine is present parallel to the stem. In a pathological *S. latus* n. sp. (Pl. 11, Fig. 12) one of the terminal spines of the wings is subdivided into two needle-like spines.

Scutispongus undulatus (DUMITRICĂ, 1982) is distinguished by the cylindrical apical spine in prolongation of an axial cylindrical elevation within the blade and stem. Moreover, the margin of the blade is stronger undulated.

Scutispongus tortilispinus n. sp. displays a strongly twisted apical spine.

Scutispongus longispinosus n. sp. displays a very long, needle-like apical spine.

Scutispongus longispinosus n. sp.
(Pl. 1, Fig. 8)

Derivation of name: According to the very long apical spine.
Holotype: The specimen on Pl. 1, Fig. 8; rep.-no. KOMO 1994 IV-127
Material: 3 specimens.
Diagnosis: Polar spine completely flattened. Stem long, narrow. Blade moderately large, subtriangular with two deep incisions above the large wings. That portion of the blade lying above the wings is a little smaller than or of the same size as the wings. Apical spine very long and except its very base needle-like. Terminal spines of wings needle-like, moderately long.
Measurements:
Length of polar spine above the shell surface (without apical spine): 200–212 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 91–97 µm

Length of straight stem above the shell: 103–109 µm
Width of straight stem in its middle part: 24 µm
Length of terminal spines of the wings: 84–103 µm
Length of apical spine: 127–133 µm
Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Scutispongus longispinosus* n. sp. is distinguished by its very long apical spine from all other *Scutispongus* species.

Scutispongus mocki n. sp.
(Pl. 13, Fig. 10)

1984 *Baumgartneria stellata* DUMITRICĂ, 1980 (sic!) – DE WEVER, p. 304, Pl. 1, Fig. 1

Derivation of name: In honour of Dr. R. MOCK, Bratislava.
Holotype: The specimen on Pl. 13, Fig. 10; rep.-no. KOMO 1994 IV-168
Type locality: Outcrop along a road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy).
Type stratum: Sample RW 13. Reddish limestone with late Cordevolian radiolarians and conodonts.
Material: 2 specimens.
Diagnosis: Polar spine completely flattened. Stem long, slender. Blade semicircular to rounded subtriangular. Terminal spines of the wings moderately long, distally needle-like. Margin of the blade smooth, except a slender triangular, distally needle-like apical spine.
Measurements:
Length of polar spine above the shell surface (without apical spine): 240–251 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 131–154 µm
Length of straight stem above the shell: 96–112 µm
Width of straight stem in its middle part: 29–31 µm
Length of terminal spines of the wings: around 160 µm (not fully preserved)
Length of apical spine: 38-40 µm

Occurrence: Very rare in the late Cordevolian at the type locality. Longobardian-Cordevolian boundary beds of the Darnó-hegy (northern Hungary).
Remarks: The blade of the polar spine is very similar to that of *Scutispongus bogdani ancoraeformis* n. subsp. which displays, however, no apical spine.

The specimen assigned by DE WEVER (1984) to *Baumgartneria stellata* DUMITRICĂ, 1982, corresponds to the new *Scutispongus* species. This form is not related to *Baumgartneria stellata* that displays terminally forked branches, whereas the form figured by DE WEVER (1984) displays an obliquely backward directed terminal spine on the wing of a bilateral blade. The sample H 198 was derived from a level above well dated latest Longobardian and below conodont proven Cordevolian. This level is already dominated by *Tritortis kretaensis kretaensis* (KOZUR & KRAHL, 1984) assigned to *Sepsagon longispinosus* ? (KOZUR & MOSTLER) and *Eptingium manfredi* DUMITRICĂ? by DE WEVER (1984). *Muelleritortis cochleata* (NAKASEKO & NISHIMURA, 1979) assigned by DE WEVER to *Plafkerium* sp. is very subordinate in this level that belongs to the *Tritortis kretaensis* Zone. Our material from this level contains conodonts that belong mostly to Paragondolella foliata BUDUROV that is common in the lower Cordevolian, but begins in the latest Longobardian. Transition forms to Paragondolella tadpole (HAYASHI) are common. This indicates rather earliest Cordevolian age.

Scutispongus ? parvifoliatus n. sp.
(Pl. 13, Fig. 6; Pl. 14, Fig. 15)

Derivation of name: According to the small blade.
Holotype: The specimen on Pl. 13, Fig. 6; rep.-no. KOMO 1994 IV-164
Material: 13 specimens.
Diagnosis: Polar spine completely flattened, but the proximal portion of the long, narrow stem is only slightly flattened. Blade small, bilateral, but asymmetric. It is situated obliquely to the polar axis and at one side distinctly higher than at the other side. One wing begins considerably higher

than the other one. At the side with the upper wing the blade may be rudimentary. External margin of the blade smooth. Terminal spines of the wings moderately long to long, needle-like, at different angle obliquely backward directed.
Measurements: See under the subspecies.
Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) and in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian). Southern Alps and Bosnia-Hercegovina.
Remarks: *Scutispongus bogdani ancoraeformis* n. subsp. displays often a similar small blade that is, however, bilaterally symmetrical.

Scutispongus reschi n. sp. displays a similar small and asymmetric blade, but it displays an eccentric apical spine and a distinct incision between the blade and one of the terminal spines.

Despite the similarity with *Scutispongus* of the *S. bogdani* group, the assignment of *Scutispongus ? parvifoliatus* n. sp. to this genus is not sure. Whereas typical *Scutispongus* evolved from *Falcispongus* DUMITRICĂ, 1982 through the transition form *Scutispongus rostratus* (DUMITRICĂ, 1982), the derivation of *Scutispongus ? parvifoliatus* n. sp. is not clear. A derivation from the *Baumgartneria curvispina* group cannot be excluded for *Scutispongus ? parvifoliatus primitivus* n. subsp. that is similar to *Baumgartneria curvispina* DUMITRICĂ, 1982, with small subtriangular blade above the stem. In this case *Scutispongus ? parvifoliatus* would be closer related to *Pterospongus* than to *Scutispongus*. However, *Baumgartneria curvispina* displays a bilateral symmetric polar spine. Because of the asymmetric blade of *Scutispongus ? parvifoliatus*, a derivation from *Falcispongus* DUMITRICĂ, 1982, cannot be excluded.

Scutispongus ? parvifoliatus parvifoliatus n. subsp.
(Pl. 13, Fig. 6)

Holotype: = holotype of the species.
Material: 3 specimens.

Diagnosis: With the character of the species. Asymmetric blade on both sides well-developed, but at the side with the upper wing somewhat smaller than at the other side. Terminal spines of both wings moderately backward directed.

Measurements:
Length of polar spine above the shell surface: 200–221 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 91–104 µm
Length of straight stem above the shell: 97–109 µm
Width of straight stem in its middle part: 20 µm
Length of terminal spines of the wings: around 160 µm (not fully preserved)

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: See also under the species.

The blade of *Scutispongus* ? *parvifoliatus primitivus* n. subsp. is at the side of the upper wing very small and the terminal spine of the upper wing is only slightly backward directed.

Scutispongus ? *parvifoliatus primitivus* n. subsp.
(Pl. 14, Fig. 15)

Derivation of name: According to the very primitive character for the genus *Scutispongus*.
Holotype: The specimen on Pl. 14, Fig. 15; rep.-no. KOMO 1994 IV-205
Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).
Type stratum: Middle part of Buchenstein Beds, sample St 1.
Material: 10 specimens.
Diagnosis: With the character of the species. Blade very small for the genus. Terminal spine of the upper wing only slightly backward directed. Terminal spine of the lower wing moderately backward directed. At the side of the upper wing, the blade is only rudimentary.

Measurements:
Length of polar spine above the shell surface: 180–187 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 75–81 µm
Length of straight stem above the shell: 107–115 µm
Width of straight stem in its middle part: 21–23 µm
Length of terminal spines of the wings: >100 µm (not fully preserved).

Occurrence: Rare in the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: See also under the species.

Scutispongus ? *parvifoliatus parvifoliatus* n. subsp. displays a larger blade that is also at the side of the upper wing well developed. The terminal spines of the wings are stronger backward directed.

Scutispongus ploechingeri n. sp.
(Pl. 3, Figs. 4, 9, 11; Pl. 4, Figs. 7, 8)

Derivation of name: In honour of Prof. B. PLÖCHINGER, Mödling.
Holotype: The specimen on Pl. 3, Fig. 9; rep.-no. KOMO 1994 IV-128
Material: More than 100 specimens.
Diagnosis: Spongy shell with few, relatively long, needle-like by-spines in the lower hemisphere, partly with needle-like antapical polar spine and short needle-like by-spines in the lower hemisphere. Apical (main) polar spine completely flattened. Stem moderately long to long, partly in its upper part rather wide. Blade large, broad, subtriangular, symmetrical or asymmetrical. Different deep, mostly shallow incisions are present on both sides, rarely only on one side of the blade. Apical end narrowly rounded to acute, but not pointed, partly somewhat separated to form a distinct to indistinct, rounded triangular, rarely triangular lobe that is often inward-bent. Inner sides of one wing or stem may display a large lobe.
Measurements: See under the subspecies.

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Scutispongus bogdani* KOLAR-JURKOVŠEK (1989) displays a broadly rounded apical end of the mostly subsemicircular blade. Incisions, if present at one side of the blade, are always very shallow and indistinct.

Scutispongus sagittaeformis n. sp. displays a arrow-like polar spine with triangular, apically pointed blade.

Scutispongus ploechingeri ploechingeri n. subsp.
(Pl. 3, Figs. 4, 9, 11)

Holotype: = holotype of the species.
Material: More than 100 specimens.
Diagnosis: With the character of the species. Spongy shell with two relatively large and one or two smaller, needle-like by-spines. One of the larger by-spines may be in the position of an antapical polar spine. Blade mostly bilateral symmetrical, rarely slightly asymmetrical. Apical end narrowly rounded to acute, with rounded triangular, rarely triangular lobe. Inner sides of wings or stem without lobe.
Measurements:
Diameter of shell: 90–125 μm
Length of polar spine above the shell surface : 214–250 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 135–145 μm
Length of straight stem above the shell: 95–115 μm
Width of straight stem in its middle part: 20–35 μm
Length of terminal spines of the wings: 125–133 μm
Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of Muelleritortis *cochleata* Zone (early late Longobardian) at the type locality.
Remarks: See also under the species.

Scutispongus ploechingeri lobatus n. subsp. displays an asymmetrical blade without apical lobe.

Scutispongus ploechingeri lobatus n. subsp.
(Pl. 4, Figs. 7, 8)

Derivation of name: According to the distinct lobe on the upper part of the stem or on the inner margin of one of the wings.
Holotype: The specimen on Pl. 4, Fig. 7; rep.-no. KOMO 1994 IV-131
Material: 9 specimens.
Diagnosis: With the character of the species. Spongy shell with small, needle-like antapical polar spine and few very small, needle-like by-spines in its lower hemisphere. The apical (main) polar spine displays a stem that considerably widens in its upper part. There may be on one side a large lobe in the upper part of the stem. Blade of the main polar spine asymmetrically triangular with acute to slightly rounded apical end that has no lobe. At one side of the blade a distinct wide and moderately deep incision is present above the wing. Terminal spines of the wings moderately long to short. These obliquely backward directed terminal spines are in their distal portion needle-like. At one side, a large lobe may be present on the inner side of the wing
Measurements:
Diameter of shell: 100-111 μm
Length of polar spine above the shell surface: 209–219 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 127–139 μm
Length of straight stem above the shell: 64–83 μm
Width of straight stem in its middle part: 33–45 μm
Length of terminal spines of the wings: 83–133 μm
Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: See also under the species.

Scutispongus ploechingeri ploechingeri n. subsp. displays an apical lobe in the position of an apical spine on the symmetrical or subsymmetrical blade. A lobe on the stem or inner side of the wings is absent.

Scutispongus reschi n. sp.
(Pl. 7, Fig. 1)

Derivation of name: In honour of Doz. Dr. W. RESCH, Innsbruck.

Holotype: The specimen on Pl. 7, Fig. 1; rep.-no. KOMO 1994 IV-113

Material: 2 specimens.

Diagnosis: Polar spine nearly completely flattened. Only the basal part of the stem is subcylindrical and only slightly flattened. Blade relatively small, asymmetrical, at one side with deep incision above the base of the terminal spine of the wing. Apical spine pointed, sidewards and somewhat inward bent, situated slightly eccentric and not directly opposite to the stem. Terminal spines of the wing needle-like, long.

Measurements:

Length of polar spine above the shell surface (without apical spine): 176–180 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 94–100 µm

Length of straight stem above the shell: 80–90 µm

Width of straight stem in its middle part: 20 µm

Length of terminal spines of the wings: 150–161 µm

Length of apical spine: 35 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: The blade is very similar to that of *Gibberospongus spinosus*, but the polar spine is unilateral in *Gibberospongus*, whereas *Scutispongus reschi* n. sp. displays a bilateral polar spine with long terminal spines on the wings at both sides. Perhaps the similarity to *Gibberospongus spinosus* is only a homeomorphy, because the stem of this species is very short to missing.

In *Scutispongus* aff. *S. reschi* n. sp. one terminal spine of the wings is short and incompletely subdivided into two needle-like spines. The other terminal spine of the wings is replaced by 3 very short needle-like spines. This form may be a pathological form of *S. reschi*, because only one specimen is present.

Scutispongus sagittaeformis n. sp.
(Pl. 9, Fig. 15; Pl. 13, Fig. 9)

Derivation of name: According to the arrow-like polar spine.

Holotype: The specimen on Pl. 13, Fig. 9; rep.-no. KOMO 1994 IV-167

Type locality: Outcrop along a road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy).

Type stratum: Sample RW 13. Reddish limestone with late Cordevolian radiolarians and conodonts.

Material: 15 specimens.

Diagnosis: Spongy shell with several small, needle-like by-spines in the lower hemisphere. Polar spine completely flattened, arrow-like. Stem long, narrow. Blade triangular with pointed apical end, but without apical spine. External margin straight or at the proximal end of the wings with incision at one side. Terminal spines moderately long, obliquely backward directed.

Measurements:

Diameter of shell: 131–155 µm

Length of polar spine above the shell surface: 200–269 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 113-173 µm

Length of straight stem above the shell: 63–100 µm

Width of straight stem in its middle part: 28–31 µm

Length of terminal spines of the wings: 138–164 µm

Occurrence: Rare from the lower *Spongoserrula fluegeli* Subzone of Muelleritortis *cochleata* Zone (early late Longobardian) to late Cordevolian. Bosnia-Hercegovina and Sicily.

Remarks: The blade in *Scutispongus ploechingeri* n. sp. is subtriangular with either an apical lobe in position of an apical spine or a lobe on the stem or inner side of one wing.

Scutispongus cf. *sagittaeformis* (Pl. 3, Fig. 8; Pl. 12, Fig. 10) is not so distinctly arrow-like and displays a horizontally wider, rather subtriangular blade with rounded external margin or the terminal spines are fewer backward directed. Partly this may be intraspecific variability (Pl. 12, Fig. 10), partly these forms are transition forms to *Scutispongus ploechingeri* n. sp. (Pl. 3, Fig. 8).

Scutispongus semifusus n. sp.
(Pl. 4, Figs. 1, 6)

Derivation of name: According to the character of the terminal wing spines.
Holotype: The specimen on Pl. 4, Fig. 6; rep.-no. KOMO 1994 IV-135
Material: 4 specimens.
Diagnosis: Spongy shell with a very small, needle-like antapical polar spine and some very small, needle-like by-spines. Apical (main) polar spine completely flattened. Stem moderately long. Blade subtriangular, slightly asymmetrical. Terminal ends of the wings needle-like. One of them is obliquely backward directed and slightly curved. The other one is backward and inward curved and its distal end joins the upper margin of the shell near the stem or the very base of the stem at the upper margin of the shell.
Measurements:
Diameter of shell: 95–100 µm
Length of polar spine above the shell surface: 215–220 µm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 100–125 µm
Length of straight stem above the shell: 95–100 µm
Width of straight stem in its middle part: 30–34 µm
Length of terminal spines of the wings: 100–160 µm
Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: In *Scutispongus bogdani* (KOLAR-JUR-KOVŠEK, 1989) the terminal spines of the wings are not inward curved to join the shell or basal part of the stem.

In *Scutispongus baloghi* n. sp. the terminal spines of both wings are backward and inward curved to join the shell or basal part of the stem.

Genus *Steigerispongus* n. gen.

Type species: *Steigerispongus subsymmetricus* n. gen. n. sp.
Diagnosis: Spongy shell with needle-like by-spines in its lower hemisphere. Main polar spine with long, straight stem that is narrow, subcylindrical, slightly flattened, rarely somewhat broader and completely flattened. The flattened blade is bilateral, mostly slightly to strongly asymmetric, on both sides ending in a generally long, needle-like, moderately to strongly recurved spine. External surface with pointed, rarely blunt, in the central part mostly long denticles. A second, needle-like polar spine may be present opposite to the flattened main polar spine.
Assigned species:
Steigerispongus subsymmetricus n. gen. n. sp.
Steigerispongus subsymmetricus subsymmetricus n. subsp.
Steigerispongus subsymmetricus fissus n. subsp.
Steigerispongus subsymmetricus latopediculus n. subsp.
Steigerispongus subsymmetricus longiaculeata n. subsp.
Spongoserrula cristagalli DUMITRICĂ, 1982
Steigerispongus asymmetricus n. sp.
Steigerispongus asymmetricus asymmetricus n. subsp.
Steigerispongus asymmetricus rectangularis n. subsp.
Steigerispongus asymmetricus triangulodentatus n. subsp.
Steigerispongus brevipediculus n. sp.
Steigerispongus ? curvispinus n. sp.
Steigerispongus dosztalyi n. sp.
Steigerispongus fojnicaensis n. sp.
Steigerispongus latofoliatus n. sp.
Steigerispongus obliquus n. sp.
Steigerispongus primus n. sp.
Steigerispongus symmetricus n. sp.
Occurrence: Common in the Longobardian and with decreasing frequency also in the Cordevolian; Tethys.
Remarks: The likewise completely flat, and except the most primitive forms denticulated blade of the polar spine in *Spongoserrula* DUMITRICĂ, 1982, is always unilateral. The straight stem is short or missing. *Spongoserrula* is the ancestral genus of *Steigerispongus*. In the strongly asymmetrical *Steigerispongus asymmetricus* n. sp. the blade is well developed on one side as in *Spongoserrula*. On the other side, a smaller, narrower and

mostly shorter blade with fewer denticles is present. This blade evolved from an especially large proximal spine on the external surface of the unilateral blade of *Spongoserrula*. As seen in *Spongoserrula fluegeli multispinosa* n. subsp., this originally obliquely upwards directed spine may downward recurve and may develop a secondary denticle on its upper margin. If this spine becomes broader and blade-like in its proximal part, the asymmetric bilateral blade of primitive *Steigerispongus* evolved. In advanced *Steigerispongus* the secondary blade becomes more and more similar to the primary one. By this at first a slightly asymmetrical bilateral blade evolved, like in *Steigerispongus subsymmetricus* n. sp. and finally bilateral symmetric forms, like *Steigerispongus symmetricus* evolved. However, the above mentioned *Spongoserrula fluegeli multispinosa* is not the direct forerunner of *Steigerispongus*. It has no long straight stem as all *Steigerispongus* species. Therefore, the direct forerunner of *Steigerispongus* should be a *Spongoserrula* species of the *S. fluegeli* group with a rather long straight stem.

Steigerispongus subsymmetricus n. gen. n. sp.
(Pl. 2, Figs. 4–7, 9-11; Pl. 10, Figs. 2–4,
7, 8, 12, 14, 15; Pl. 12, Figs. 16–18)

Derivation of name: According to the subsymmetrical, slightly asymmetrical blade of the polar spine.
Holotype: The specimen on Pl. 2, Fig. 7; rep.-no. KOMO 1994 IV-50
Material: More than 100 specimens.
Diagnosis: Spongy shell with a bunch of needle-like by-spines near the antapical pole and a large, flattened apical polar spine. The polar spine displays a long, subcylindrical, somewhat flattened to broad and completely flattened stem. The blade is broad, bilateral, subsymmetrical, slightly asymmetrical. One side of the blade begins mostly in a higher level of the stem than the other side. If the blade begins on both sides of the stem in the same level, one side of the blade is broader. The 4–6 denticles are long, slender, pointed.

They are largest in the middle part of the blade and their length decreases toward both distal ends of the blade. The distal denticles on both sides are often very low, rounded triangular or reduced to a slight undulation. Opposite to the stem lies mostly a interspine space, but there may be also the largest spine opposite to the stem. This spine may be terminally bifurcated. The number of spines may be on both sides of the blade equal, but often on one side there are one, rarely two denticles fewer than on the other side. Both distal ends of the blade are terminated by a long to very long, narrow, needle-like spine that is obliquely backward directed to a different degree. In general, the distal ends of these terminal spines are situated in the level of the equator to lower pole of the shell.
Measurements: See under the subspecies.
Occurrence: Very common in the late Longobardian of the Tethys.
Remarks: *Steigerispongus cristagalli* (DUMITRICĂ, 1982) displays flattened cylindrical denticles with blunt ends.

Steigerispongus symmetricus n. sp. and *S. brevipediculus* n. sp. display a symmetrical or nearly symmetrical blade with three symmetrically arranged denticles. *S. brevipediculus* has additionally a short stem.

Steigerispongus asymmetricus n. sp. and *S. obliquus* n. sp. display a very asymmetric blade.

Steigerispongus subsymmetricus subsymmetricus n. subsp.
(Pl. 2, Figs. 4, 7, 11; Pl. 10, Figs. 2, 4, 7, 8 14;
Pl. 12, Figs. 16–18)

Derivation of name, holotype and occurrence: As for the species.
Material: More than 100 specimens.
Diagnosis: With the character of the species. Straight stem long, narrow. All spines unbranched, long. Opposite to the stem, there is an interspine space and only exceptionally an unbranched spine. The terminal spines of the wings are strongly backward directed.

Measurements:
Diameter of shell: 119–125 μm
Length of polar spine above the shell surface (without denticles): 140–193 μm
Maximum width of polar spine (distance from inner to outer margins of the blade): 62–88 μm
Length of straight stem above the shell: 78–100 μm
Width of straight stem in its middle part: 22–28 μm
Length of terminal spines of the wings: 125–233 μm
Maximum length of denticles: 66–82 μm
Occurrence: Common in the *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (late Longobardian) of the Tethys.
Remarks: See also under the species.

In *Steigerispongus longidentatus* n. subsp. the 3–4 proximal spines on the external margin of the blade are very large and the needle-like distal terminal spines of the wings are slightly to moderately backward directed. They terminate above the level of the shell.

Steigerispongus subsymmetricus latopediculus n. subsp. displays a broad, completely flattened, long, straight stem and the denticles are rather short.

Steigerispongus subsymmetricus fissus n. subsp. displays a terminally bifurcated spine opposite to the stem.

Steigerispongus subsymmetricus fissus n. subsp.
(Pl. 10, Figs. 3, 15)

Derivation of name: According to the distally furcated spine opposite to the stem.
Holotype: The specimen on Pl. 10, Fig. 3; rep.-no. Komo 1994 IV-57
Material: 7 specimens.
Diagnosis: With the character of the species. Straight stem narrow, short to moderately long. Opposite to the stem lies a distally bifurcated spine on the external margin of the blade. Distal terminal spines of the wings rather short, moderately to strongly backward directed, partly terminally bifurcated.
Measurements:
Length of polar spine above the shell surface (without denticles): 131–200 μm

Maximum width of polar spine (distance from inner to outer margins of the blade): 85–94 μm
Length of straight stem above the shell: 63–107 μm
Width of straight stem in its middle part: 25–27 μm
Length of terminal spines of the wings: around 100 μm
Maximum length of denticles: 91-94 μm
Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: See also under the species.

Steigerispongus subsymmetricus fissus n. subsp. is distinguished from the other subspecies of *Steigerispongus subsymmetricus* by the distally bifurcated spine opposite to the stem and by the rather short stem.

Steigerispongus subsymmetricus latopediculus n. subsp.
(Pl. 2, Figs. 5, 6, 10)

Derivation of name: According to the broad, flattened stem.
Holotype: The specimen on Pl. 2, Fig. 10; rep.-no. Komo 1994 IV-53
Material: 13 specimens.
Diagnosis: With the character of the species. Straight stem broad, long and completely flattened. Denticles on the external side of the stem relatively short.
Measurements:
Length of polar spine above the shell surface (without denticles): 165–210 μm
Maximum width of polar spine (distance from inner to outer margins of the blade): 70–90 μm
Length of straight stem above the shell: 90–120 μm
Width of straight stem in its middle part: 39–51 μm
Length of terminal spines of the wings: 144–157 μm
Maximum length of denticles: 42-60 μm
Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Steigerispongus subsymmetricus latopediculus* n. subsp. is distinguished from other

subspecies of *Steigerispongus subsymmetricus* n. sp. by its completely flattened, broad stem. In *Steigerispongus* cf. *subsymmetricus latopediculus* n. subsp. (Pl. 2, Fig. 9) the stem begins above the shell as narrow as in *Steigerispongus subsymmetricus subsymmetricus* n. subsp., but it widens distinctly in direction to the blade. This form may be a transitional form between *Steigerispongus subsymmetricus subsymmetricus* and *S. subsymmetricus latopediculus*.

Steigerispongus subsymmetricus longiaculeatus n. subsp.
(Pl. 10, Figs. 8, 12)

? 1984 *Falcispongus* sp.- DE WEVER, Pl. 3, Fig. 6

Derivation of name: According to the very long proximal spines on the external margin of the blade.

Holotype: The specimen on Pl. 10, Fig. 8; rep.-no. KOMO 1994 IV-62

Material: 4 specimens.

Diagnosis: With the character of the species. Proximal spines on the external margin of the blade very long. Distal terminal needle-like spine of the wings only slightly to moderately backward directed.

Measurements:

Length of polar spine above the shell surface (without denticles): about 200 μm (proximal part of the stem in none of the specimens preserved).

Maximum width of polar spine (distance from inner to outer margins of the blade): 100–120 μm

Width of straight stem in its middle part: 30–35 μm

Length of terminal spines of the wings: 325–345 μm

Maximum length of spines: 150–219 μm

Occurrence: Very rare in the *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (late Longobardian) and in the basal Tritortis kretaensis Zone (Longobardian-Cordevolian boundary level) of Bosnia-Hercegovina and Hungary.

Remarks: *Steigerispongus subsymmetricus longiaculeatus* n. subsp. is distinguished from other subspecies of *Steigerispongus subsymmetricus* by its very long proximal denticles. Moreover, the terminal needle-like spine of the wings is only slightly to moderately backward directed.

Steigerispongus asymmetricus n. sp.
(Pl. 2, Fig. 8; Pl. 11, Figs. 2-8, 11; Pl. 13, Fig. 7)

Derivation of name: According to the bilateral, but strongly asymmetrical blade.

Holotype: The specimen on Pl. 11, Fig. 4; rep.-no. KOMO 1994 IV-67

Material: More than 100 specimens.

Diagnosis: Straight stem slender, long, rarely moderately long, subcylindrical, slightly flattened. Blade completely flattened, bilateral, but strongly asymmetrical. Main blade (primary blade) large, moderately broad, rarely narrow, always strongly recurved. Terminal spine needle-shaped of the wings short to moderately long, ending in the level of the central or upper part of the shell. External margin of main blade with 5–6 mostly slender, terminally needle-like spines that distalwards decrease in size. Distal one-two denticles rather short, triangular, sometimes reduced to an undulation of the external margin. In *S. asymmetricus triangulodentatus* n. subsp. all denticles of the main blade are rather short and triangular. Secondary blade considerably smaller, narrower, with one-two small to large spine on its external margin. The secondary blade is either perpendicularly to the stem or recurved. It begins always in a lower level of the stem than the main blade. Terminal spine of the wings needle-like, short to long.

Measurements: See under the subspecies.

Occurrence: Common in the *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (late Longobardian) and in the Cordevolian of the Tethys.

Remarks: *Steigerispongus asymmetricus* n. sp. is the most primitive *Steigerispongus* species with transition character to *Spongoserrula* DUMITRICĂ, 1982. The main (primary) blade corresponds to the blade of *Spongoserrula* of the *S. fluegeli* group. The much smaller secondary blade is partly not yet downward curved and bears only one denticle. It has clearly developed from an especially large

proximal spine in *Spongoserrula*, which may have exceptionally already a tiny spine (*Spongoserrula fluegeli multispinosa* n. subsp.), but is not yet widened to a flat blade in *Spongoserrula*.

On the other hand, there are also transition forms to *Steigerispongus subsymmetricus* (Pl. 11, Fig. 2; Pl. 13, Fig. 7), in which the secondary blade becomes somewhat larger and displays two-three denticles. In these forms the asymmetry of the blade is not more so strong as in typical *Steigerispongus asymmetricus*.

cle. In *S. asymmetricus triangulodentatus* additionally the denticles of the main blade are short and triangular, whereas *S. asymmetricus rectangularis* displays a rather short stem.

In *Steigerispongus* cf. *asymmetricus asymmetricus* n. subsp. (Pl. 11, Fig. 8) the rather large spine on the secondary blade is terminally bifurcated.

Steigerispongus asymmetricus subsp. indet. (Pl. 11, Fig. 11) displays a narrow main blade, not wider than the secondary blade.

Steigerispongus asymmetricus asymmetricus n. subsp.
(Pl. 2, Fig. 8; Pl. 11, Figs. 4, 5, 7)

Holotype: As for the species.
Material: 83 specimens.
Diagnosis: With the character of the species. Stem long. Main blade with long, terminally needle-like spines. Only distal spines of main blade triangular. The secondary blade with long, needle-like terminal spine is always recurved. It begins in a considerably lower level of the stem than the main blade.
Measurements:
Length of polar spine above the shell surface (without denticles): 145–167 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 56–70 µm
Length of straight stem above the shell: 55–78 µm
Width of straight stem in its middle part: 20–25 µm
Length of terminal spine of the wings: 94–118 µm
Maximum length of spines of the main blade: 59–85 µm
Maximum length of spines of the secondary blade: 22–55 µm
Occurrence: Common in the *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (late Longobardian) and in the Cordevolian of the Tethys.
Remarks: See also under the species.

In *Steigerispongus asymmetricus rectangularis* n. subsp and *S. asymmetricus triangulodentatus* n. sp. the short secondary blade is situated perpendicularly to the stem and bears only a small denti-

Steigerispongus asymmetricus rectangularis n. subsp.
(Pl. 11, Fig. 6; Pl. 13, Fig. 3)

Derivation of name: According to the right angle between the stem and secondary blade.
Holotype: The specimen on Pl. 11, Fig. 6; rep.-no. KOMO 1994 IV-73
Material: 9 specimens.
Diagnosis: With the character of the species. Stem relatively short. Secondary blade short with a small pointed spine and a rather short needle-like terminal prolongation, perpendicularly to the stem. Proximal denticles of the main blade long, needle-shaped, only basally broader. Needle-like terminal spine of the main blade rather short.
Measurements:
Length of polar spine above the shell surface (without denticles): 152–160 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 69–75 µm
Length of straight stem above the shell: 45–53 µm
Width of straight stem in its middle part: 26–30 µm
Length of terminal spine of the main blade: 91–133 µm
Length of terminal spine of the secondary blade: 73–77 µm
Maximum length of spines of the main blade: 95–147 µm
Maximum length of spines of the secondary blade: 22–25 µm
Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: In *Steigerispongus asymmetricus asymmetricus* n. subsp. the secondary blade is longer and recurved. The stem is longer.

Steigerispongus asymmetricus triangulodentatus n. subsp. has a longer stem and shorter, triangular proximal denticles on the main blade.

Steigerispongus asymmetricus triangulodentatus n. subsp.
(Pl. 11, Fig. 3)

Derivation of name: According to the triangular denticles on the main blade.
Holotype: The specimen on Pl. 11, Fig. 3; rep.-no. KOMO 1994 IV-72
Material: 3 specimens.
Diagnosis: With the character of the species. The secondary blade is very short with short terminal spine and a very small rounded triangular denticle.
Measurements:
Length of polar spine above the shell surface (without denticles): 140–145 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 55–60 µm
Length of straight stem above the shell: 72–78 µm
Width of straight stem in its middle part: 20–22 µm
Length of terminal spine of the secondary blade: 25–30 µm
Maximum length of denticles on the main blade: 28-31 µm
Maximum length of denticle on the secondary blade: 10–13 µm
Occurrence: Very rare in the middle Longobardian at the type locality.
Remarks: See also under the species.

The secondary blade of *Steigerispongus asymmetricus asymmetricus* n. subsp. is larger, recurved and its distal part is obliquely backwards directed. The proximal spines on the main blade are long and terminally needle-like.

In *Steigerispongus asymmetricus rectangularis* n. subsp. the size and arrangement of the secondary blade is similar, but the stem is longer and the proximal spines on the main blade are long and terminally needle-like.

Steigerispongus brevipediculus n. sp.
(Pl. 2, Fig. 3)

Derivation of name: According to the short stem.
Holotype: The specimen on Pl. 2, Fig. 3; rep.-no. KOMO 1994 IV-76
Material: 4 specimens.
Diagnosis: Spongy shell slightly spiny, with few needle-like by-spines, mostly arranged in a bunch somewhat beside the antapical pole. Polar spine completely flattened. Stem short for the genus and rather broad. Blade very broad, nearly bilateral-symmetrical. 3 spines are present in the apical region of the blade arranged in a line perpendicularly to the polar axis. The largest, needle-like spines lies opposite to the stem. The other two spines are shorter, broader, but also pointed. They are symmetrically arranged on both sides of the middle spine. In distal direction of these spines on each side a further, short, rounded triangular denticle or shall node is present. The terminal spine of the wings are symmetrically arranged, sword-like, obliquely backward directed. They end in the level of the upper part of the shell.
Measurements:
Diameter of shell: 122–139 µm
Length of polar spine above the shell surface (without denticles): 144–156 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 83–94 µm
Length of straight stem above the shell: 41–56 µm
Width of straight stem in its middle part: 42–46 µm
Length of the terminal spine of the wings: 106–139 µm
Maximum length of spines: 83-97 µm
Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: *Steigerispongus symmetricus* n. sp. displays a long, slender stem. The denticles are shorter, the terminal spine of the wings is needle-

like and mostly longer. All other *Steigerispongus* species display asymmetric blades.

Steigerispongus ? *curvispinus* n. sp.
(Pl. 10, Fig. 9; Pl. 11., Fig. 10)

Derivation of name: According to the strongly sidewards curved large spine on the external margin of the blade.

Holotype: The specimen on Pl. 11, Fig. 10; rep.-no. KOMO 1994 IV-64

Material: 3 specimens.

Diagnosis: Polar spine with somewhat flattened, large, narrow straight stem and completely flattened, strongly asymmetric bilateral, spined blade. One side of the blade (main blade) is downward curved and terminates in a long, needle-like, strongly downward directed terminal spine. This main blade displays 3 spines on its external margin. The proximal one is very large, the other two are considerably smaller. The large spine is laterally curved toward the other side of the blade (secondary blade), where it is fused with the only denticle of the secondary blade or reaches beyond this denticle a short distance above it. By this arrangement and shape of the adjacent denticles on the main and secondary blades a partly open pore or incision in the blade is formed. The secondary blade is smaller to much smaller than the main blade, obliquely upward directed and only the terminal spine is downward curved (but this terminal part is broken away after its very base in all present specimens). A denticle on the proximal end of the external margin of the secondary blade is fused with the laterally curved part of the large spine on the main blade or it ends somewhat below it.

Measurements:
Length of polar spine above the shell surface (without denticles): 173–178 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 67–80 µm
Length of straight stem above the shell: 80–83 µm
Width of straight stem in its middle part: 28–30 µm
Length of terminal spine of the wings: Around 200 µm

Length of curved spine (including the curved part): 93–200 m
Maximum length of the other spines: 33-56 µm
Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of the *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Steigerispongus* ? *curvispinus* n. sp. is distinguished from all other described *Steigerispongus* species by the laterally curved largest spine on the external margin of the blade. By the partly open pore or incision opposite to the stem, this species is similar to *Pterospongus* DUMITRICA, 1982. However, this is probably only a homeomorph feature, because this pore or incision developed by the sidewards bending of the largest proximal spine and it is not an original feature of the blade as in *Pterospongus*. On the other side, there is a considerable similarity with Spongoserrula DUMITRICA, 1982. However, the blade is already bilateral, but strongly asymmetrical. Moreover, the straight stem is long.

Steigerispongus ? *curvispinus* n. sp. probably belongs to the *Steigerispongus asymmetricus* group, in which the second blade is still very different from the main (primary) blade.

Steigerispongus asymmetricus n. sp. has no laterally curved spine and the secondary blade lies either perpendicularly to the stem or it is obliquely downward directed.

Steigerispongus dosztalyi n. sp.
(Pl. 12, Figs. 13, 14)

Derivation of name: In honour of Dr. L. DOSZTÁLY, Budapest.

Holotype: The specimen on Pl. 12, Fig. 13; rep.-no. KOMO 1994 IV-153

Material: 10 specimens.

Diagnosis: Spongy shell with needle-like antapical polar spine. Main (apical) polar spine flattened, with relatively small blade. Stem long, narrow, basally not flattened, distally flattened. The rather narrow blade is bilateral asymmetric. It is situated obliquely to the polar axis. At one side, the

·wing begins considerably higher than at the other side. Both wings ends in terminal, moderately long to long, needle-like spines that are obliquely backward directed. Two node-like, rounded, small denticles are present in the apical portion of the blade, but they may be shifted in a more lateral position.

Measurements:
Diameter of spongy shell: 100–115 μm
Length of polar spine above the shell surface (without denticles): 189–197 μm
Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 54–69 μm
Length of straight stem above the shell: 93–106 μm
Width of straight stem in its middle part: 20–29 μm
Length of terminal spine of the wings: 106–118 μm
Maximum length of denticles: 21–24 μm

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Steigerispongus fojnicaensis* n. sp. displays three denticles and at one side the terminal spine of the wing lies parallel to the stem.

Steigerispongus obliquus n. sp. displays three pointed, distally needle-like spines.

Steigerispongus fojnicaensis n. sp.
(Pl. 10, Figs. 10, 13)

Derivation of name: According to the occurrence in the locality Varoski creek near Fojnica, Bosnia-Hercegovina.

Holotype: The specimen on Pl. 10, Fig. 10; rep.-no. KOMO 1994 IV-84

Material: 11 specimens.

Diagnosis: Spongy shell with a bunch of needle-like, short by-spines near to the antapical pole. Stem long, narrow, in its upper part often slightly curved. Blade obliquely to the polar axis, bilateral, asymmetrical, with 3 rounded denticles. One of these denticles may be reduced to a tiny node. The denticles are arranged in a line, oblique to the polar axis. The central spine is not situated in the polar axis. It is always the largest denticle. Dis-

talwards from these denticle a small, shallow lobe may be present on the external margin of the blade. Terminal spine of the wings long, needle-like. At one side of the blade the terminal spine is obliquely backward directed and ends in the level of the upper part of the shell. At the other side of the blade the terminal spine is strongly backward curved and ends also in the level of the upper part of the shell. It is situated parallel to the stem. Sometimes at one side two terminal needle-like spines are present. One of them is situated parallel to the stem, the other one is obliquely backward directed and may join the middle part of the stem.

Measurements:
Diameter of shell: 131–138 μm
Length of polar spine above the shell surface (without denticles): 180–200 μm
Maximum width of polar spine (distance from inner to outer margins of the blade): 77–100 μm
Length of stem above the shell: 83–131 μm
Width of stem in its middle part: 28–34 μm
Length of obliquely backward direct terminal spines: 145–164 μm
Length of the backward recurved terminal spine: 100–115 μm
Maximum length of denticles: 27–38 μm

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: On that side, where the terminal spine of the wing is situated parallel to the stem, a second terminal spine may be present that is obliquely inward directed and joins the stem. This form may represent an independent subspecies, but so far only one specimen with bifurcated terminal spine at one wing is present among 11 specimens of *Steigerispongus fojnicaensis* n. sp.

In *Steigerispongus obliquus* n. sp. the denticles are pointed and both terminal spines of the wings are obliquely backward directed.

Steigerispongus dosztalyi n. sp. displays only two rounded spines and both terminal spines of the wings are obliquely backward directed. Moreover, this species has a needle-like antapical spine.

Steigerispongus latofoliatus n. sp.
(Pl. 11, Fig. 1)

Derivation of name: According to the very wide secondary blade.

Holotype: The specimen on Pl. 11, Fig. 1; rep.-no. KOMO 1994 IV-77

Material: 6 specimens.

Diagnosis: Stem of polar spine short, subcylindrical, slightly flattened. Blade completely flattened, bilateral, but very asymmetric. One side is moderately wide, rather long, terminated in a moderately long, needle-like spine. This side corresponds to the main (primary) blade of other asymmetric *Steigerispongus* species. Other side shorter, very broad, with very short terminal spine. This side corresponds to the secondary blade of other asymmetrical *Steigerispongus* species. External margin spined. The denticulation on the primary blade is regular, with two large, needle like proximal spines and two considerably smaller, subtriangular distal denticles. The denticulation on the secondary blade is rather irregular. Proximally a long, needle-like spine is present. The distalwards following 3 denticles are very small to small, but their size may increase toward the distal end. The denticle opposite to the stem is in general small and triangular.

Measurements:
Length of polar spine above the shell surface (without denticles): 163–175 µm
Maximum width of polar spine (distance from inner to outer margins of the blade): 81–100 µm
Length of straight stem above the shell: 29–32 µm
Width of straight stem in its middle part: 25–28 µm
Length of distal terminal spine of the wings: 44–62 µm
Maximum length of spines: 63–94 µm

Occurrence: Very rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Steigerispongus latofoliatus* n. sp. is distinguished from other *Steigerispongus* species with strongly asymmetric bilateral blade by the very broad secondary blade, which is distinctly broader than the primary blade.

Steigerispongus obliquus n. sp.
(Pl. 10, Figs. 1, 11)

Derivation of name: According to the oblique blade and the obliquely arranged denticles.

Holotype: The specimen on Pl. 10, Fig. 11; rep.-no. KOMO 1994 IV-82

Material: 31 specimens.

Diagnosis: Polar spine totally flattened. Stem long. Blade obliquely to the polar axis, bilateral, asymmetrical, with 3 pointed denticles. The denticles are arranged in a line, oblique to the polar axis. The central denticle is the largest one, or all three denticles have equal length. The terminal spines of the wings are long, needle-like, obliquely backward directed. They end at one side in the level of the upper part of the shell, at the other side somewhat above it.

Measurements:

Occurrence: Common in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Steigerispongus symmetricus* n. sp. displays a bilateral symmetric blade. The 3 denticles are arranged in a line perpendicularly to the polar axis. *S.* cf. *symmetricus* n. sp. displays a slightly oblique blade and one side of the blade is very strongly recurved. This form may be a transition form between *S. symmetricus* n. sp. and *S. obliquus* n. sp. Similar to it are such forms of *S. obliquus*, in which the blade is not strongly oblique (Pl. 10, Fig. 1).

Steigerispongus subsymmetricus n. sp. has more denticles and the outline of the blade is different.

Steigerispongus fojnicaensis n. sp. displays the same shape and arrangement of the blade. The 3 denticles display, however, rounded ends and on one side the terminal spine of the wing is strongly backward curved and lies parallel to the stem.

Steigerispongus primus n. sp.
(Pl. 15, Fig. 11)

Derivation of name: Stratigraphically oldest *Steigerispongus* species of the *S. cristagalli* group.

Holotype: The specimen on Pl. 15, Fig. 11; rep.-no. Komo 1994 IV-198

Locus typicus: Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994).

Type stratum: Middle part of Buchenstein Beds, sample St 1.

Material: 3 specimens.

Diagnosis: Spongy shell relatively large. Straight stem moderately long. Blade very small, bilateral, asymmetric. One wing with moderately long, obliquely backward directed terminal spine. The other wing with short terminal spine, perpendicularly to the stem. Two short, rounded denticles in apical position.

Measurements:

Diameter of spongy shell: 144–156 µm

Length of polar spine above the shell surface (without apical spine): 138–144 µm

Maximum width of polar spine (maximum distance from inner to outer margins of the blade): 62–63 µm

Length of straight stem above the shell: 63 µm

Width of straight stem in its middle part: 31 µm

Length of long terminal spine of wings: 106–109 µm

Length of short terminal spine of wings: 31–38 µm

Maximum length of denticles: 19–25 µm

Occurrence: Very rare in the lower subzone (*Pterospongus priscus* Subzone) of the *Muelleritortis cochleata* Zone (early middle Longobardian) at the type locality.

Remarks: *Steigerispongus cristagalli* (DUMITRICĂ, 1982) from the middle subzone (*Spongoserrula rarauana* Subzone) of the *Muelleritortis cochleata* Zone (middle Longobardian) displays more and longer denticles and an almost symmetrical, larger blade.

Steigerispongus sp. A displays three denticles, two of them with pointed end. One terminal spine is long and strongly backward curved.

Steigerispongus symmetricus n. sp
(Pl. 2, Figs. 1, 2)

Derivation of name: According to the symmetric or nearly symmetric polar spine.

Holotype: The specimen on Pl. 2, Fig. 2; rep.-no. Komo 1994 IV-78

Material: 17 specimens.

Diagnosis: Spongy shell slightly spiny, in the lower hemisphere with several needle-like by-spines, that may be partly arranged in a bunch. Straight stem very long, subcylindrical, slightly flattened. Blade completely flattened, bilaterally symmetrical or nearly so. On the apical end of the blade three triangular to slender triangular denticles are arranged in a straight line perpendicularly to the polar axis. The middle denticle of them, situated opposite to the stem, is the largest, the other two are symmetrically arranged on both sides of the central denticle and somewhat shorter; occasionally one of these denticles may be reduced to a node. Distalward from these three spines a partly indistinct node may be present on both sides of the blade. The terminal spines on both sides of the blade are long and strongly backward directed. Their ends are situated in the level of the central to upper parts of the shell.

Measurements:

Diameter of shell: 89–106 µm

Length of polar spine above the shell surface (without denticles): 178–194 µm

Maximum width of polar spine (distance from inner to outer margins of the blade): 56–75 µm

Length of straight stem above the shell: 100–111 µm

Width of straight stem in its middle part: 19–25 µm

Length of terminal spine of the wings: 111–194 µm

Maximum length of denticles: 28–39 µm

Occurrence: Rare in the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.

Remarks: *Steigerispongus* cf. *symmetricus* n. sp. (Pl. 10, Fig. 5) displays a slightly oblique bilateral blade. The denticles terminate in a needle-like spine. The recurvation of the terminal spines of the blade is very strong and its distal end may reach on one side the margin of the shell. Moreover, a distinct, rather long and needle like antapical polar spine is present. This latter feature indicates that *Steigerispongus* cf. *symmetricus* n. sp. may belong at least to an independent subspecies, which is similar to *Steigerispongus* ? sp. A, in which, however, the blade is strongly reduced at one side to a broad, rounded teeth. From this form only one specimen

is present (Pl. 10, Fig. 6), that may be a pathological form. By the reduction of the blade at one side, this form is homeomorph to *Spongoserrula* DUMITRICĂ, 1982 that has, however, a short stem.

Steigerispongus brevipediculus n. sp. has a similar denticulation, but a higher blade and a shorter stem.

Steigerispongus subsymmetricus n. sp. has a slightly asymmetric blade which bears more denticles.

Steigerispongus obliquus n. sp. displays an oblique, asymmetric blade. The denticles are similarly arranged as in *S. symmetricus*, but in a line distinctly oblique to the polar axis.

Steigerispongus ? sp. A
(Pl. 10, Fig. 6)

Material: One specimen.
Occurrence: Lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian) at the type locality.
Remarks: It is not clear, whether the long proximal spine of the blade is a spine of an unilateral blade (in this case the specimen would belong to *Spongoserrula* DUMITRICĂ, 1982) or a reduced terminal spine of a wing of a bilateral blade (similar to Steigerispongus primus n. sp.).

Steigerispongus sp. B
(Pl. 7, Fig. 4)

Remarks: Only one specimen is known from a *Steigerispongus* species, in which all 4 spines are laterally and (or) inward curved. It may be a pathological form.

Steigerispongus sp. C
(Pl. 13, Fig. 11)

Remarks: A single, not fully preserved specimen of a *Steigerispongus* species with very short trian-

gular stem is known from the Cordevolian of Sicily. It represents surely a new species distinguished by the very short, rapidly widening triangular stem from other species of the *Steigerispongus fluegeli* group.

Biostratigraphic evaluation

The Oertlispongidae KOZUR & MOSTLER, 1980, are the stratigraphically most important Ladinian radiolarians of pelagic deposits in the tropical Tethyan sea. In the Circum-Pacific realm Oertlispongidae are also present, but mostly rare. Because the curved and often bladelike modified, partly denticulated or spined apical polar spine is the most significant and rapidly evolving feature of the Oertlispongidae, isolated apical polar spines can be well determined in species or even subspecies level.

As shown in KOZUR & MOSTLER (1994) and DOSZTÁLY (1994), Oertlispongidae with curved main (apical) polar spine began at the priority base of the Ladinian stage (base of the *Reitziites reitzi* Zone), where also distinct changes in ammonoids, conodont and sporomorph associations can be observed. This boundary is therefore most suitable as Anisian-Ladinian boundary and can be recognized not only in ammonoid-bearing beds (about 5% of the Triassic rocks near the Anisian-Ladinian boundary), but also in continental beds (more than 50% of the beds in this stratigraphic interval) and in radiolarites, where ammonoids are missing and conodonts (if present in such beds) are mostly represented by juvenile specimens unsuitable for detailed stratigraphic evaluations.

As shown by KOZUR & MOSTLER (1994), the Fassanian Oertlispongidae are characterized by an unilateral or bilateral curved apical polar spine without blade-like differentiation (*Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER, 1980, *Baumgartneria* DUMITRICĂ, 1982) or by an unilateral curved apical polar spine with blade-like widenings at the distal end of straight stem and the very base of the curved portion of the polar spine.

Whereas *Baumgartneria* is a rather conservative genus, rapid evolution within *Oertlispongus* and partly also within *Falcispongus* allows detailed stratigraphic subdivisions of the Fassanian (see KOZUR & MOSTLER, 1994).

Within the Longobardian advanced Oertlispongidae evolved. They are characterized by completely flattened apical polar spines with bilateral, smooth, denticulated or spined blades, partly with apical incision (*Pterospongus* DU-MITRICĂ, 1982, *Scutispongus* n. gen., *Steigerispongus* n. gen.) or by denticulated unilateral blades (*Spongoserrula* DUMITRICĂ, 1982). Rapid evolution within these genera allows a subdivision of the middle to late Longobardian *Muelleritortis cochleata* Zone (contemporaneous with the *Budurovignathus mungoensis* conodont zone) into 3 subzones, defined below. Advanced *Baumgartneria*, *Falcispongus* and *Oertlispongus* are with decreasing frequency present up to the middle subzone of the *Muelleritortis cochleata* Zone (middle Longobardian). Exceptionally, last advanced *Oertlispongus* occur in the upper subzone of the *M. cochleata* Zone (late Longobardian). Additionally the very characteristic corkscrew-like twisted *Bogdanella* KOLAR-JURKOVŠEK, 1989 is present in the entire Longobardian.

In the Cordevolian advanced Oertlispongidae are present with decreasing frequency. Partly they range up from the late Longobardian upper subzone of *M. cochleata* Zone (*Scutispongus sagittaeformis* n. sp., *Steigerispongus asymmetricus* n. sp.), partly they represent species not yet present in the Longobardian (*Scutispongus mocki* n. sp., *Steigerispongus* sp. C). The first occurrences of *Spongoserrula dehli* CORDEY et al. and *Spongoserrula cordeyi* n. sp., common in the Cordevolian, are not yet clear. They may begin in the latest Longobardian, but are characteristic forms of the Cordevolian.

Occurrences of Oertlispongidae in the Tuvalian (DUMITRICĂ, 1982) cannot be confirmed.

In the following, three new subzones of the middle to late Longobardian *Muelleritortis cochleata* Zone will be introduced. In the definition only Oertlispongidae are considered.

Pterospongus priscus Subzone

Definition: Common occurrence of *Pterospongus priscus* n. sp., *P. altofissus* n. sp., *Scutispongus rostratus* DUMITRICA, 1982 (primitive *Scutispongus* with only a terminal spine only at one wing), advanced *Baumgartneria* (*B. curvispina* DUMITRICA, 1982), advanced *Falcispongus* (*F. hamatus* DUMITRICĂ, 1982, *F. falciformis minor* n. subsp., *F. transitus brevifoliaceus* n. subsp.) and *Bogdanella praecursor* n. sp. Denticulated *Spongoserrula* are missing, denticulated *Steigerispongus* with round denticles (*S. parvifoliatus primitivus* n. sp.) are very rare.

Lower boundary: Appearance of *Pterospongus priscus* n. sp., *P. latofissus* n. sp., primitive *P. alatus* DUMITRICĂ, 1982, *Bogdanella praecursor* n. sp., *Falcispongus transitus brevifoliaceus* n. subsp., *Steigerispongus primus* n. sp.

Upper boundary: First appearance of *Spongoserrula* with round or blunt denticles (*S. rarauana* group).

Present Oertlispongidae (see table 1).

Age: Lower subzone of *Muelleritortis cochleata* Zone. Lower part of *Budurovignathus mungoensis* conodont zone (early middle Longobardian).

Occurrence: Tethys and Philippines.

Remarks: This subzone represent the beginning of the Longobardian radiation of advanced Oertlispongidae. Some Fassanian guideforms (e.g. *Oertlispongus inaequispinosus* DUMITRICA, KOZUR & MOSTLER, 1980, are still present. The typical Longobardian and Cordevolian *Scutispongus* is already common, but mostly represented by transition forms to *Falcispongus* in which the terminal wing spine is only present at one side of the blade (*Scutispongus rostratus*). Exceptionally primitive *Scutispongus* with terminal spines at both sides of the blade are present, but they have an asymmetric small blade. Very primitive *Steigerispongus* with round spines (*S. cristagalli* group) are rarely present (*Steigerispongus primus* n. sp.) and undenticulated *Spongoserrula* made their first appearance.

Especially characteristic of the *Pterospongus priscus* Subzone is the rich occurrence of *Pterospongus*. This genus occurs also in the following

Spongoserrula rarauana Subzone, but with other species (*Pterospongus incissus* DUMITRICĂ, 1982, *P. patrulii* DUMITRICĂ, 1982). *Pterospongus alatus* DUMITRICĂ, 1982 is already present, but with primitive forms that probably belong to a different subspecies.

Spongoserrula rarauana Subzone

Definition: Occurrence of denticulated *Spongoserrula* with round or blunt spines (*Spongoserrula rarauana* group) and denticulated *Steigerispongus* with round spines [*Steigerispongus cristagalli* (DUMITRICĂ, 1982)] without *Spongoserrula* with pointed spines (*S. fluegeli* group) and without spined *Steigerispongus* with pointed or needle-like spines (*Steigerispongus subsymmetricus* group). Occurrence of last primitive *Scutispongus* (*S. rostratus* group) and of advanced *Pterospongus* (*P. alatus* DUMITRICĂ, 1982, *P. incissus* DUMITRICĂ, 1982, *P. patrulii* DUMITRICĂ, 1982).

Lower boundary: First appearance denticulated *Spongoserrula* with round or blunt denticles (*S. rarauana* group).

Upper boundary: First appearance of *Spongoserrula* with pointed or needle-like spines (*Spongoserrula fluegeli* group).

Present Oertlispongidae: See table 1.

Age: Middle subzone of *Muelleritortis cochleata* Zone. Upper part of lower *Budurovignathus mungoensis* conodont zone (middle Longobardian).

Occurrence: Tethys.

Remarks: This subzone is characterized by denticulated Oertlispongids with round or blunt denticles, e. g. *Spongoserrula rarauana* DUMITRICĂ, 1982, *Steigerispongus cristagalli* (DUMITRICĂ, 1982), whereas *Spongoserrula* and *Steigerispongus* with pointed or needle-like spines are still missing. For the last time primitive *Scutispongus* with only one terminal spine are present (*Scutispongus rostratus* group). Advanced *Pterospongus* (*P. alatus* DUMITRICĂ, 1982, *P. incissus* DUMITRICĂ, 1982, *P. patrulii* DUMITRICĂ, 1982) are also characteristic and this genus has its stratigraphi-

cally youngest occurrence in the *Spongoserrula rarauana* Subzone.

Spongoserrula fluegeli Subzone

Definition: Occurrence of several *Spongoserrula* and *Steigerispongus* species with pointed or needle-like denticles or spines, e. g. *Spongoserrula fluegeli* n. sp., *Spongoserrula goricanae* n. sp. *Steigerispongus asymmetricus* n. sp., *Steigerispongus subsymmetricus* n. sp., *Steigerispongus symmetricus* n. sp. together with advanced *Scutispongus*, e. g. *Scutispongus bogdani* (KOLAR-JURKOVŠEK, 1989), *Scutispongus latus* n. sp., *Scutispongus ploechingeri* n. sp., *Scutispongus longispinosus* n. sp., *Scutispongus tortilispinus* n. sp., and several *Gibberospongus* species (*Gibberospongus spinosus* n. gen. n. sp., *Gibberospongus bispinosus* n. sp., *Gibberospongus kraineri* n. sp., *Gibberospongus tichyi* n. sp.).

Lower boundary: First appearance of *Spongoserrula fluegeli* n. sp., *Steigerispongus subsymmetricus* n. sp. and other *Spongoserrula* and *Steigerispongus* species with pointed or needle-like denticles or spines. First appearance of *Gibberospongus*.

Upper boundary: = Upper boundary of the *Muelleritortis cochleata* Zone. Sudden drastic drop in the frequency of *M. cochleata* (NAKASEKO & NISHIMURA, 1979) and beginning dominance of *Tritortis kretaensis kretaensis* KOZUR & KRAHL, 1984. First appearance of *Palaeosaturnalis*.

Present Oertlispongidae: See table 1.

Age: Upper Subzone of the *Muelleritortis cochleata* Zone, late Longobardian.

Occurrence: Tethys, Philippines, western North America.

Remarks: In the *Spongoserrula fluegeli* Subzone, the maximum diversity of advanced Oertlispongidae can be observed. *Gibberospongus* seems to be restricted to this subzone. Other characteristic forms, like *Steigerispongus asymmetricus* and *Scutispongus sagittaeformis* n. sp. reaches into the Cordevolian *Tritortis kretaensis* Zone that is dominated by *Spongoserrula dehli* CORDEY et al., 1988,

Subzones:	Middle-late Longobardian			Cordevolian
	Muelleritortis cochleata Zone			Tritortis kretaensis Zone
	P. priscus	S. rarauana	S. fluegeli	undivided
Baumgartneria curvispina	XXXXXXXXXX	00000000000		
Baumgartneria dumitricae		00000000000		
Bogdanella bosniensis			00000	
Bogdanella cordevolica				000000000000
Bogdanella praecursor	XXXXXXXXXX	00000000000		
Bogdanella trentana balkanica			XXXXX	
Bogdanella trentana trentana			++++++++	
Falcispongus falciformis minor	0000000000	00000000000	???????????	000
Falcispongus hamatus	XXXXXXXXXX	+++++000000		
Falcispongus transitus brevifoliaceus	XXXXXXXXXX	???????????	00000	
Falcispongus transitus transitus			XXXXX	
Gibberospongus bispinosus			00000	
Gibberospongus kraineri			+++++	
Gibberospongus spinosus			XXXXX	
Gibberospongus tichyi			00000	
Oertlispongus deweveri			00000	
Oertlispongus inaequispinosus	<++++00000	???		
Paroertlispongus ? lobatus			00000	
Pterospongus alatus	000000	++++++00000		
Pterospongus altofissus	0000000000			
Pterospongus aquilus		00000000000		
Pterospongus incissus		00000000000		
Pterospongus patrulii		+++++++++++		
Pterospongus parvifissus	XXXXXXXXXX			
Pterospongus priscus priscus	XXXXXXXXXX			
Pterospongus priscus tortilis	+++++++++++			
Scutispongus alienus			o	
Scutispongus baloghi			oo	
Scutispongus bicornutus			oo	
Scutispongus bituberosus			oo	
Scutispongus bogdani ancoraeformis			XXXXX	
Scutispongus bogdani bogdani			XXXXXXXXXX	
Scutispongus cephalus			oo	
Scutispongus dumitricai			oo	
Scutispongus gackoensis			oo	
Scutispongus gracilispinosus			oo	
Scutispongus latus			XXXXXXXXXX	
Scutispongus longispinosus			oo	
Scutispongus mocki				00000000000000000000000000000
Scutispongus ? parvifoliatus parvifoliatus			00000	
Scutispongus ? parvifoliatus primitivus	+++++++++++			
Scutispongus ploechingeri lobatus			+++++	
Scutispongus ploechingeri ploechingeri			XXXXXXXXXX	
Scutispongus reschi			oo	
Scutispongus rostratus incurvatus	0000000000			
Scutispongus rostratus minutispinus	000000			
Scutispongus rostratus rostratus	<XXXXXXXXX	++++++00000		
Scutispongus sagittaeformis			00000000000	+++++++++++++++++++++++++++++
Scutispongus semifusus			00000	
Scutispongus tortilispinus			XXXXXXXXXX	
Scutispongus undulatus		++++++	XXXXXXXXXX	

Table 1: Distibution of Oertlispongidae in the *Muelleritortis cochleata-Tritortis kretaensis* zones (middle Longobardian to Cordevolian)
x = common, + = rare, o = very rare, ? = assumed, but unproven
< = also present in older Ladinian beds

	Middle-late Longobardian			Cordevolian
	Muelleritortis cochleata Zone			Tritortis kretaensis Zone
Subzones:	P. priscus	S. rarauana	S. fluegeli	undivided
Spongoserrula antiqua	0000000000			
Spongoserrula bidentata		00000000000	00000	
Spongoserrula bifurcata bifurcata			00000	
Spongoserrula bifurcata parvispina			00	
Spongoserrula bipolaris			00	
Spongoserrula cordeyi			?	xxxxxxxxxxxxx0000000
Spongoserrula dehli			??	xxxxxxxxxxxxxxxx++++++++++
Spongoserrula falcata			+++++	
Spongoserrula fluegeli fluegeli			xxxxxx+++++	
Spongoserrula fluegeli multispinosa			00	
Spongoserrula goricanae			+++++++++++	
Spongoserrula nuda			00	
Spongoserrula ornata			00	
Spongoserrula rarauana rarauana		00++xxxxxxx	xx+++000	
Spongoserrula rarauana trinodosa		+++++++++++	00000	
Spongoserrula raridenticulata			00000	
Spongoserrula semicircularis			00000	
Steigerispongus asymmetricus asymmetricus			xxxxxxxxxx	xxxxxx++++++++++++++++00000
Steigerispongus asymmetricus rectangularis			+++++++++++	
Steigerispongus asymmetricus triangulodentatus			00000	
Steigerispongus brevipediculus			00000	
Steigerispongus cristagalli		+++++++++++		
Steigerispongus ? curvispinus			00	
Steigerispongus dosztalyi			+++++	
Steigerispongus fojnicaensis			+++++	
Steigerispongus latofoliatus			00000	
Steigerispongus obliquus			xxxxxxxxxx	
Steigerispongus primus	0000000000			
Steigerispongus ? sp. A			0	
Steigerispongus sp. B			0	
Steigerispongus sp. C				0
Steigerispongus subsymmetricus fissus			00000	
Steigerispongus subsymmetricus latopediculus			+++++000000	
Steigerispongus subsymmetricus longiaculeatus			00000000000	??
Steigerispongus subsymmetricus subsymmetricus			xxxxxxxxxx	
Steigerispongus symmetricus			+++++++++++	

Table 1 (continued)

and *Spongoserrula cordeyi* n. sp. (first appearance of these two species perhaps in the upper *Spongoserrula fluegeli* Subzone). Only 4 Cordevolian species are so far known that are unknown from the *Spongoserrula fluegeli* Subzone, but may begin in its upper, not yet well known part: *Bogdanella cordevolica* n. sp., *Scutispongus mocki* n. sp., *Spongoserrula cordeyi* n. sp. and *Steigerispongus* sp. C. A lot of species of the *Spongoserrula fluegeli* Subzone are not known from the Cordevolian. However, we have only investigated rich well preserved radiolarian faunas from the upper Cordevolian, where Oertlispongidae are already rare. The lower Cordevolian faunas of the Darnostly represented by juvenileOertlispongidae, but mostly broken specimens, difficult to determine. Like the faunas of the upper *Spongoserrula fluegeli* Subzone, they are dominated by *Spongoserrula* and *Steigerispongus* with pointed or needle-like spines, but with other species than in the *Spongoserrula fluegeli* Subzone (*Spongoserrula dehli* CORDEY et al., 1988, *S. cordeyi* n. sp.). *Gibberospongus* is not

more present and *Scutispongus* is very rare and only represented by *Scutispongus sagittaeformis* n. sp. and *Scutispongus mocki* n. sp. The Oertlispongidae show therefore at the upper boundary of the *Spongoserrula fluegeli* Subzone a distinct decrease in diversity and only few forms begin new in the Cordevolian. The stratigraphic importance of the Oertlispongidae is therefore in the Cordevolian considerably smaller than in the Ladinian. One of the stratigraphically most important Cordevolian (and entire Late Triassic) radiolarians are the Parasaturnalidae that have evolved from the Oertlispongidae.

Our investigated Longobardian samples with Oertlispongidae are partly rich in conodonts, partly conodonts are missing or very rare. Sample 88-272 from Bosnia-Hercegovina yielded a few *Buduro-vignathus mungoensis* (DIEBEL). Therefore it belongs to the *B. mungoensis* conodont zone, but its position within this zone cannot be determined by conodonts. The presence of *Spongoserrula* and *Steigerispongus* with pointed or needle-like spines is characteristic of the *Spongoserrula fluegeli* Subzone of late Longobardian age. The genus *Tritortis* KOZUR & KRAHL is still rare in this sample which is clearly dominated by *Muelleritortis*. Therefore, the uppermost *Muelleritortis cochleata* Zone (upper *Spongoserrula fluegeli* Subzone) can be excluded for this sample. For this reason, the sample belongs to the lower *Spongoserrula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian).

The exact age of this sample within the *Muelleritortis cochleata* Zone could not be determined by Hungarosaturnalidae, because these radiolarians are so far only described from scattered occurrences within the *Muelleritortis cochleata* Zone and the phylogenetic lines within the Hungarosaturnalidae are not yet well known. Therefore this sample was erroneously placed into the lower *Muelleritortis cochleata* Zone by MOSTLER & KRAINER (1994).

The conodont-free sample Bi 1 from Bielschitza Mt. (Karawanken Mountains, southern Austria) was assigned to the uppermost Longobardian by MOSTLER & KRAINER (1994) because it lies immediately below the Schlern Dolomite which is placed into the Carnian with a local beginning in the latest

Cordevolian. However, the sample Bi 1 belongs to the middle Longobardian *Spongoserrula rarauana* Subzone. Therefore the Schlern Dolomite begins locally within the middle Longobardian.

These two examples show the importance of the Longobardian Oertlispongidae for detailed stratigraphic assignment of beds that have no conodonts or conodont zonal index forms that do not allow a subdivision of the conodont zone. Sometimes the radiolarians are better suitable for stratigraphic assignments than the conodonts. Thus, the radiolarian sample investigated by CORDEY et al. (1988) from British Columbia was by conodonts placed into the Late Anisian to Early Ladinian. The radiolarian fauna, however, indicates clearly the presence of the lower *Tritortis kretaensis* Zone. The *Tritortis kretaensis* Zone characterizes the Cordevolian and does not begin before the latest Longobardian. The presence of *Tritortis kretaensis kretaensis* (KOZUR & KRAHL, 1984), *Spongoserrula dehli* CORDEY et al. and *Spongoserrula cordeyi* n. sp. excludes any age older than late Longobardian. The latter two species are advanced representatives of the *Spongoserrula fluegeli* group (*Spongoserrula* with pointed or needle-like spines) that does not begin before the late Longobardian. *Tritortis kretaensis kretaensis* does not begin before the late Longobardian as well. A Late Anisian to Early Ladinian age can be therefore definitely excluded, even if we take into consideration that the Anisian-Ladinian boundary is placed at the base of the *Eoprotrachyceras* fauna in North America.

The radiolarian zonation based on Oertlispongidae is more detailed than the ammonoid- and conodont zonations. Like in the Fassanian, also the Longobardian subzones can be still further subdivided at least in lower and upper parts. However, the subzones are defined here as wide as possible to assign also poor radiolarian faunas without difficulties.

Acknowledgements

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Authors' addresses:
Dr. sc. Heinz Kozur, Rézsü u. 83, H-1029 Budapest, Hungary; Univ.-Prof. Dr. Helfried Mostler, Institute of Geology and Paleontology, University of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria.

Explanation of Plates

All specimens for which no locality and age data are given were derived from sample 88-272 from the locality Varoski creek near Fojnica, Republic Bosnia-Hercegovina. They belong to the lower *Spongoser-rula fluegeli* Subzone of *Muelleritortis cochleata* Zone (early late Longobardian).

Plate 1

Figs. 1–3: *Scutispongus latus* n. sp.; Fig. 1: holotype, x 200, rep.-no. KOMO 1994 IV-123; Fig. 2: x 160, rep.-no. KOMO 1994 IV-124; Fig. 3: x 200, rep.-no. KOMO 1994 IV-125.

Figs. 4-6: *Scutispongus undulatus* (DUMITRICA, 1982); Fig. 4: x 170, rep.-no. KOMO 1994 IV-99; Fig. 5: x 180, rep.-no. KOMO 1994 IV-100; Fig. 6: x 170, rep.-no. KOMO 1994 IV-101.

Figs. 7, 9–11: *Scutispongus tortilispinus* n. sp.; Fig. 7: x 150, rep.-no. KOMO 1994 IV-94; Fig. 9: x 170, rep.-no. KOMO 1994 IV-95; Fig. 10: x 150, rep.-no. KOMO 1994 IV-96; Fig. 11: holotype, x 200, rep.-no. KOMO 1994 IV-93.

Fig. 8: *Scutispongus longispinosus* n. sp., holotype, x 165, rep.-no. KOMO 1994 IV-127.

Plate 2

Plate 3

Figs. 1, 2, 5, 6: *Scutispongus bogdani bogdani* (KOLAR-JURKOVŠEK, 1989); Fig. 1: x 180, rep.-no. KOMO 1994 IV-105; Fig. 2: x 150, rep.-no. KOMO 1994 IV-106; Fig. 5: x 180, rep.-no. KOMO 1994 IV-107; Fig. 6: x 200, rep.-no. KOMO 1994 IV-138.

Figs. 3, 10: *Scutispongus bogdani ancoraeformis* n. subsp.; Fig. 3: x 230, rep.-no. KOMO 1994 IV-110; Fig. 10: x 200, rep.-no. KOMO 1994 IV-111.

Figs. 4, 9, 11: *Scutispongus ploechingeri ploechingeri* n. subsp.; Fig. 4: x 210, rep.-no. KOMO 1994 IV-129; Fig. 9: holotype, x 200, rep.-no. KOMO 1994 IV-128; Fig. 11: x 200, rep.-no. KOMO 1994 IV-130.

Fig. 7: *Scutispongus* cf. *bogdani bogdani* (KOLAR-JURKOVŠEK, 1989), transition form to *Scutispongus ploechingeri* n. sp., x 180, rep.-no. KOMO 1994 IV-104.

Fig. 8: *Scutispongus* cf. *sagittaeformis* n. sp., transition form to *Scutispongus ploechingeri* n. sp., x 200, rep.-no. KOMO 1994 IV-137.
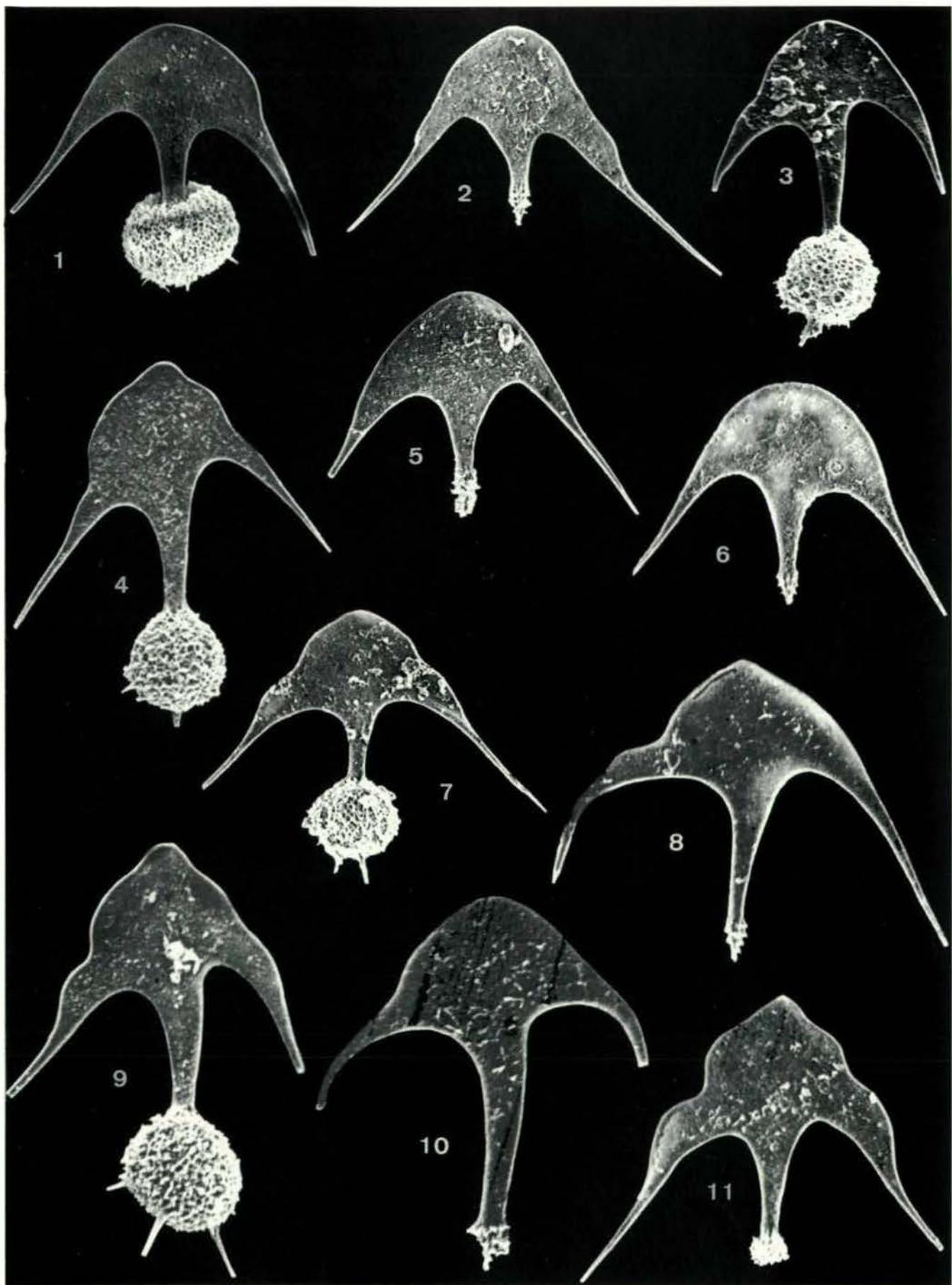
Plate 4

Figs. 1, 6:   *Scutispongus semifusus* n. sp.; Fig. 1: x 250, rep.-no. KOMO 1994 IV-236; Fig. 6: holotype, x 200, rep.-no. KOMO 1994 IV-235.

Fig. 2:   *Scutispongus bogdani bogdani* (KOLAR-JURKOVŠEK, 1989), x 180, rep.-no. KOMO 1994 IV-108.

Fig. 3:   *Scutispongus* cf. *latus* n. sp., x 300, rep.-no. KOMO 1994 IV-122.

Fig. 4:   *Scutispongus* cf. *bogdani ancoraeformis* n. subsp., x 300, rep.-no. KOMO 1994 IV-112.

Figs. 5, 10:   *Scutispongus baloghi* n. sp.; Fig. 5: holotype, x 220, rep.-no. KOMO 1994 IV-114; Fig. 10: x 170, rep.-no. KOMO 1994 IV-115.

Figs. 7, 8:   *Scutispongus ploechingeri lobatus* n. subsp.; Fig. 7: holotype, x 220, rep.-no. KOMO 1994 IV-131; Fig. 8: x 180, rep.-no. KOMO 1994 IV-132.

Fig. 9:   *Scutispongus bogdani ancoraeformis* n. subsp., holotype, x 180, rep.-no. KOMO 1994 IV-109.

Fig. 11:   *Scutispongus dumitricai* n. sp., holotype, x 180, rep.-no. KOMO 1994 IV-120.
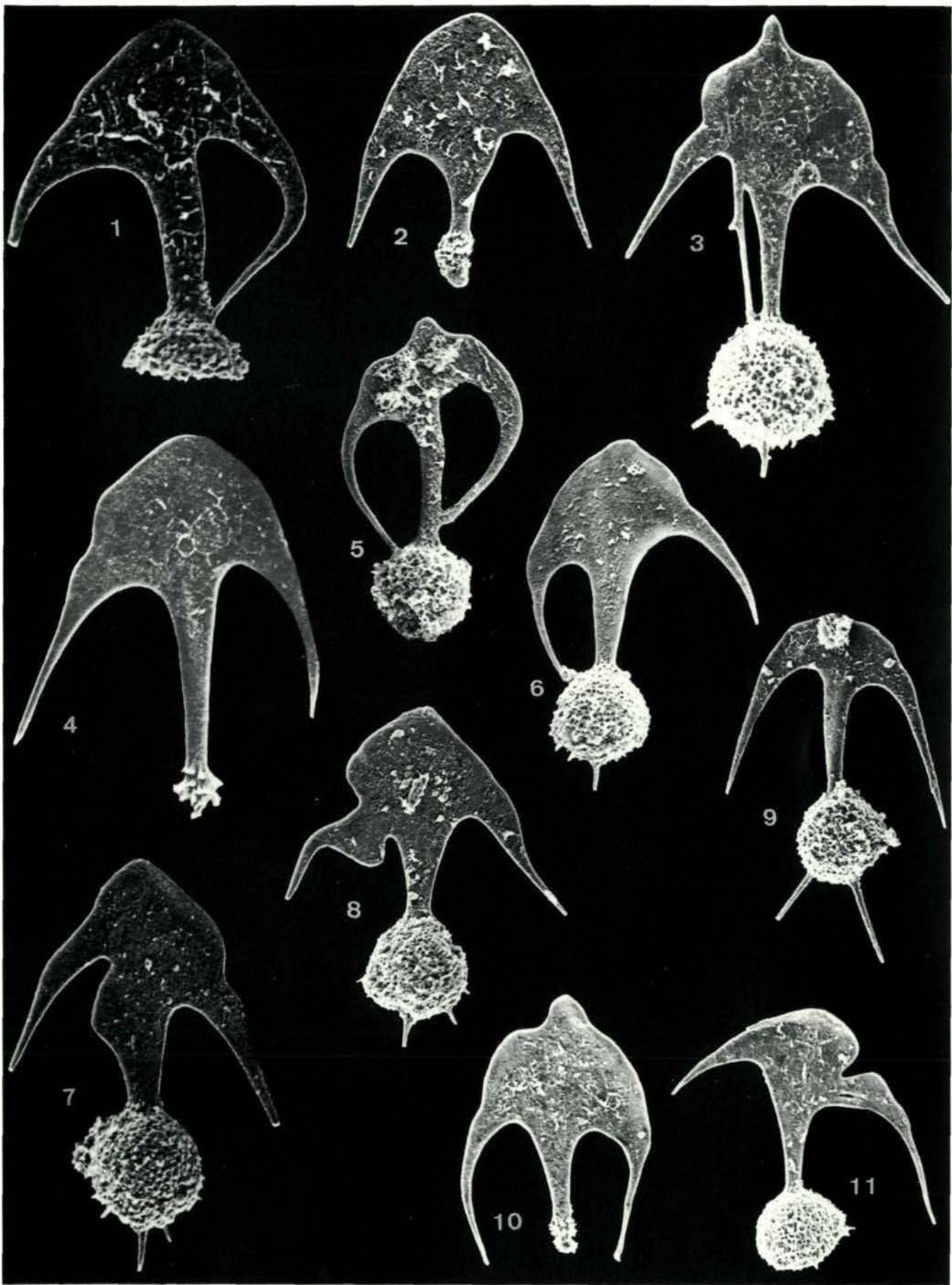
Plate 5

Fig. 1:   *Spongoserrula ornata* n . sp., holotype, x 180, rep.-no. KOMO 1994 IV-38.

Figs. 2, 3, 5, 6: *Spongoserrula falcata* n. sp.; Fig. 2: holotype, x 170, rep.-no. KOMO 1994 IV-32; Fig. 3: x 220, rep.-no. KOMO
                1994 IV-33; Fig. 5: x 220, rep.-no. KOMO 1994 IV-34; Fig. 6: x 260, rep.-no. KOMO 1994 IV-35.

Figs. 4, 7:   *Spongoserrula bifurcata bifurcata* n. subsp. ; Fig. 4: x 180, rep.-no. KOMO 1994 IV-39; Fig. 7: holotype, x 180,
                rep.-no. KOMO 1994 IV-40.

Fig. 8:   *Spongoserrula rarauana trinodosa* n. subsp., holotype, x 175, rep.-no. KOMO 1994 IV-36.

Fig. 9:   *Spongoserrula bidentata* n. sp., holotype, x 170, rep.-no. KOMO 1994 IV-41.

Figs. 10, 11,   *Spongoserrula rarauana rarauana* DUMITRICĂ, 1982; Fig. 10: x 180, rep.-no. KOMO 1994 IV-21; Fig. 11:

13, 14:   x 180, rep.-no. KOMO 1994 IV-22; Fig. 13: x 170, rep.-no. KOMO 1994 IV-23; Fig. 14: x 170, rep.-no. KOMO
                1994 IV-24.

Fig. 12:   *Spongoserrula* cf. *rarauana trinodosa* n. subsp., transition form between *S. rarauana trinodosa* n. subsp. and *S.
                rarauana rarauana* DUMITRICĂ, 1982, x 170, rep.-no. KOMO 1994 IV-37.

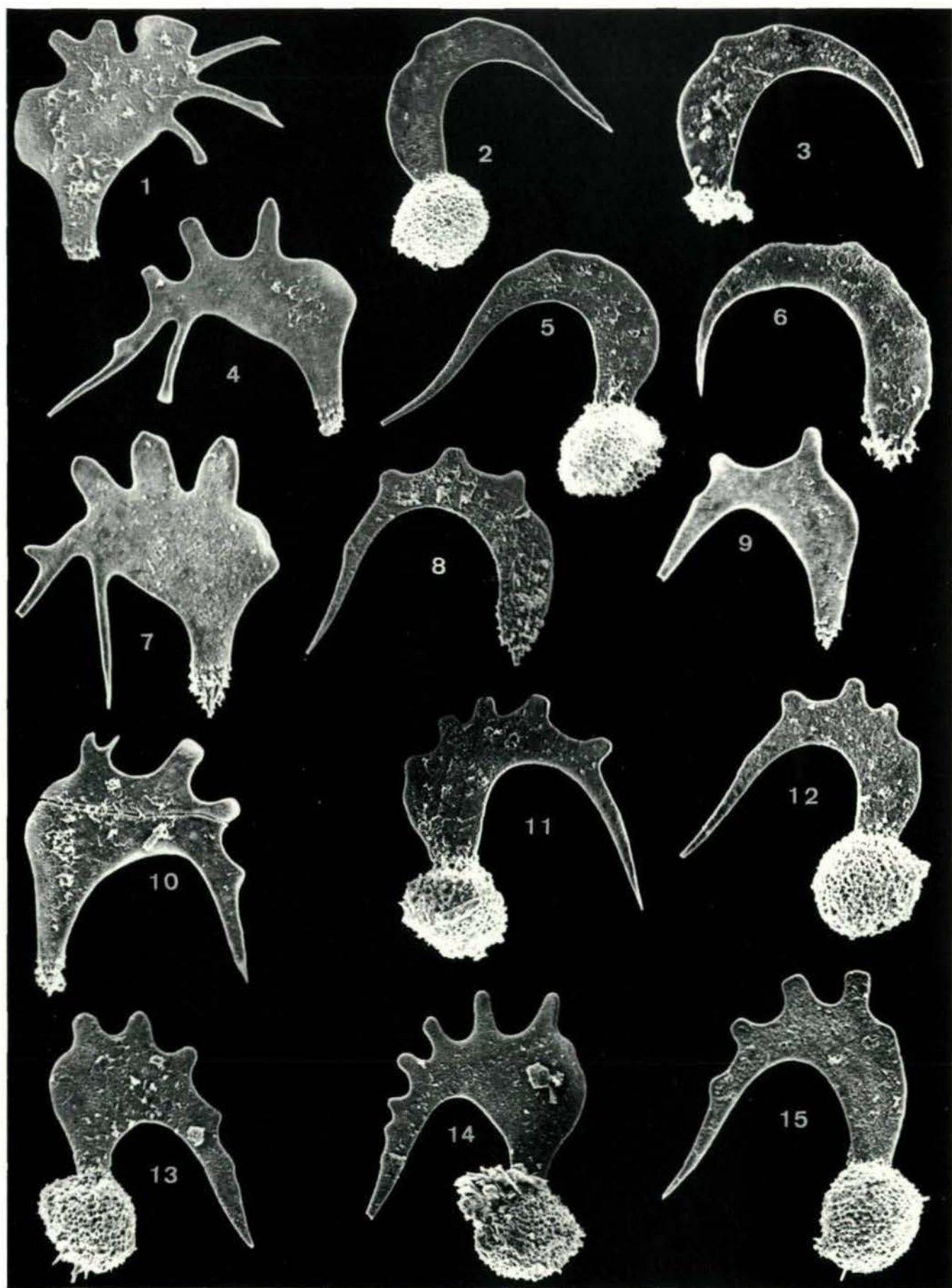Fig. 15:   *Spongoserrula* cf. *rarauana rarauana* DUMITRICĂ, 1982, x 170, rep.-no. KOMO 1994 IV-25.

Plate 6

Figs. 1–3, 6, 9: *Spongoserrula rarauana rarauana* DUMITRICĂ, 1982; Fig. 1: x 180, rep.-no. KOMO 1994 IV-26; Fig. 2: x 180, rep.-no. KOMO 1994 IV-27; Fig. 3: x 250, rep.-no. KOMO 1994 IV-28; Fig. 6: x 200, rep.-no. KOMO 1994 IV-29; Fig. 9: x 170, rep.-no. KOMO 1994 IV-30.

Fig. 4:   *Spongoserrula bipolaris* n. sp., holotype, x 140, rep.-no. KOMO 1994 IV-44.

Figs. 5, 7, 8, 11: *Spongoserrula fluegeli fluegeli* n. subsp.; Fig. 5: x 160, rep.-no. KOMO 1994 IV-46; Fig. 7: x 150, rep.-no. KOMO 1994 IV-47; Fig. 8: holotype, x 220, rep.-no. KOMO 1994 IV-45; Fig. 11: x 180, rep.-no. KOMO 1994 IV-48.

Fig. 10:   *Spongoserrula fluegeli multispinosa* n. subsp., holotype, x 140, rep.-no. Komo 1994 IV-49.
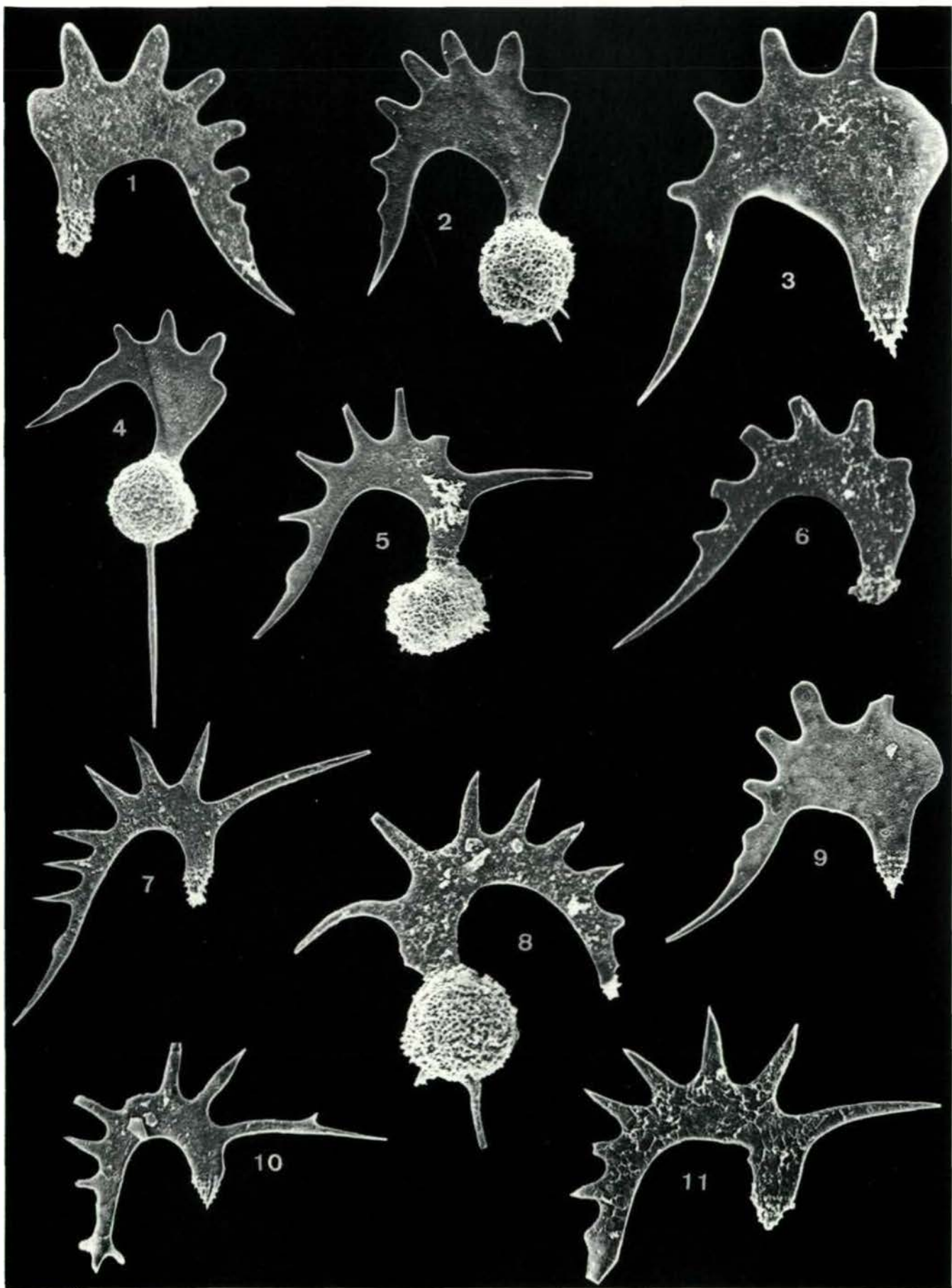
Plate 7

Fig. 1:   *Scutispongus reschi* n. sp., holotype, x 200, rep.-no. Komo 1994 IV-113.

Fig. 2:   *Scutispongus gracilispinosus* n. sp., holotype, x 180, rep.-no. Komo 1994 IV-115.

Fig. 3:   *Scutispongus alienus* n. sp., holotype, x 180, rep.-no. Komo 1994 IV-116.

Fig. 4:   *Steigerispongus* sp. B, x 160, rep.-no. Komo 1994 IV-63.

Fig. 5:   *Oertlispongus deweveri* n. sp., holotype, x 200, rep.-no. Komo 1994 IV-1.

Fig. 6:   *Bogdanella bosniensis* n. sp., holotype, x 300, rep.-no. Komo 1994 IV-87.

Figs. 7–9, *Bogdanella trentana balkanica* n. subsp.; Fig. 7: holotype, x 200, rep.-no. Komo 1994 IV-88; Fig. 8: x 200,
12, 13:   rep.-no. Komo 1994 IV-89; Fig. 9: x 200, rep.-no. Komo 1994 IV-92; Fig. 12: x 250, rep.-no. Komo 1994 IV-90;
            Fig. 13: x 250, rep.-no. Komo 1994 IV-91.

Fig. 10:   *Spongoserrula* sp., x 250, rep.-no. Komo 1994 IV-66.

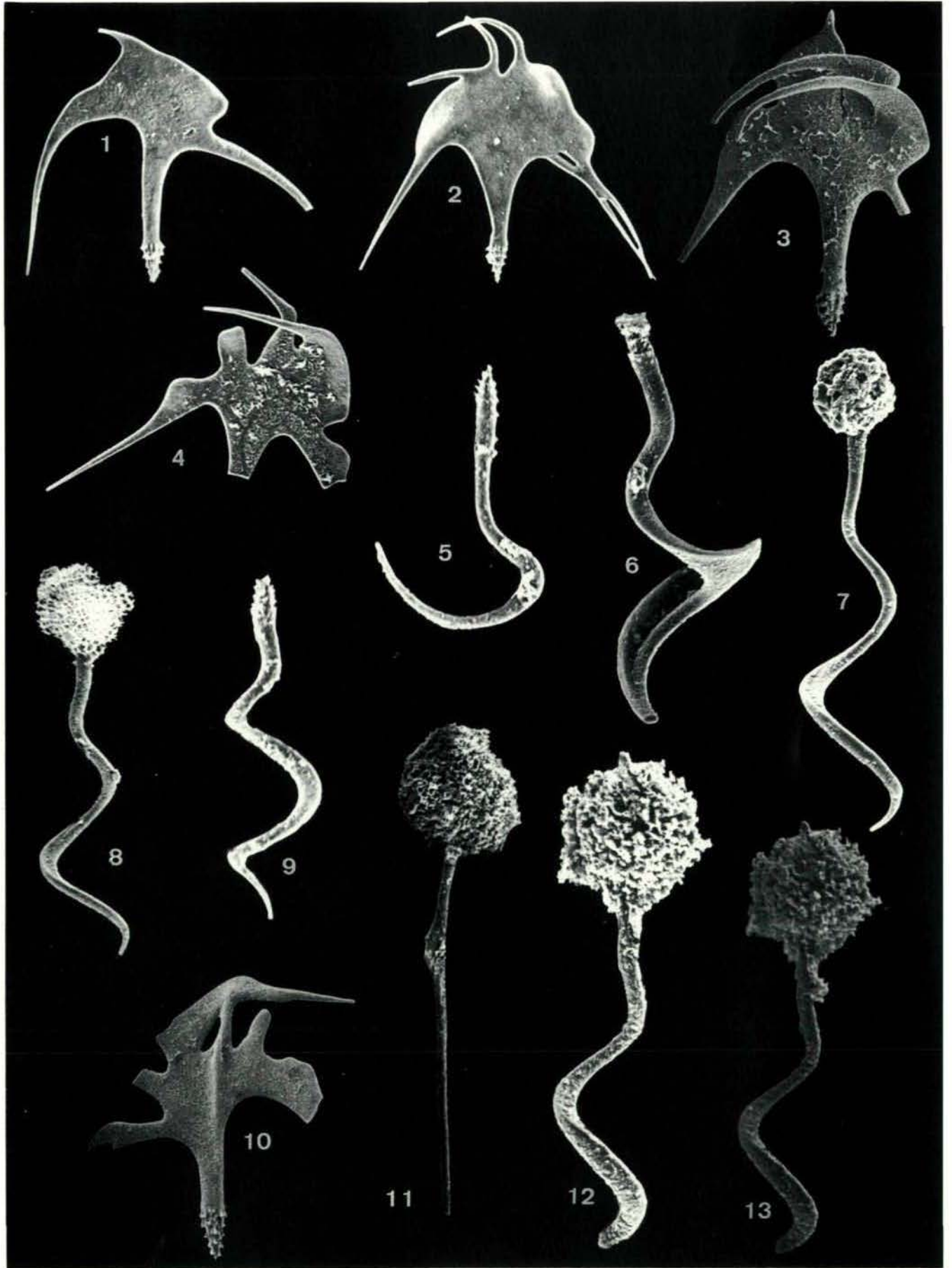Fig. 11:   *Paroertlispongus* ? *lobatus* n. sp., holotype, x 250, rep.-no. Komo 1994 IV-86.

Plate 8

Fig. 1: *Gibberospongus kraineri* n. sp., x 200, rep.-no. KOMO 1994 IV-3.

Fig. 2: *Falcispongus* aff. *F. transitus* n. sp., x 230, rep.-no. KOMO 1994 IV-4.

Fig. 3: *Falcispongus transitus brevifoliaceus* n. subsp., holotype, x 400, rep.-no. KOMO 1994 IV-8.

Fig. 4: *Scutispongus latus* n. sp., x 250, rep.-no. KOMO 1994 IV-126.

Fig. 5: *Spongoserrula* cf. *rarauana* DUMITRICĂ, 1982, x 130, rep.-no. KOMO 1994 IV-140.

Fig. 6: *Gibberospongus spinosus* n. sp., x 200, rep.-no. KOMO 1994 IV-17.

Figs. 7, 8: *Scutispongus tortilispinus* n. sp.; Fig. 7: x 220, rep.-no. KOMO 1994 IV-97; Fig. 8: x 220, rep.-no. KOMO 1994 IV-98.

Fig. 9: *Spongoserrula rarauana rarauana* DUMITRICĂ, 1982, x 250, rep.-no. KOMO 1994 IV-102.

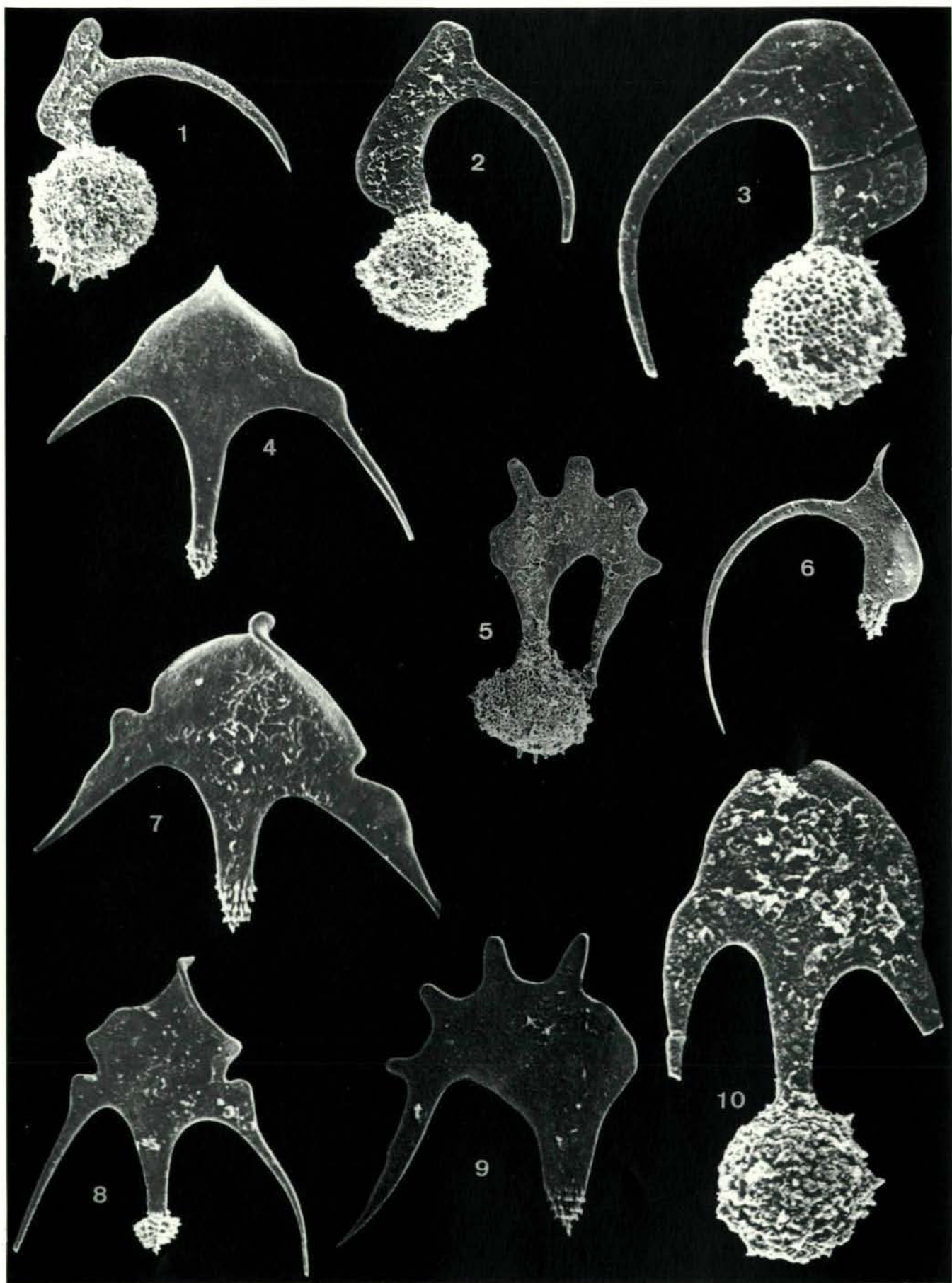Fig. 10: *Scutispongus bogdani bogdani* (KOLAR-JURKOVŠEK, 1989), x 400, rep.-no. KOMO 1994 IV-103.

Plate 9

Figs. 1, 5: *Falcispongus hamatus* DUMITRICĂ, 1982; Fig. 1: x 180, rep.-no. KOMO 1994 IV-10; Fig. 5: x 200, rep.-no. KOMO 1994 IV-11.

Fig. 2: *Gibberospongus tichyi* n . sp., holotype, x 180, rep.-no. KOMO 1994 IV-20.

Fig. 3: *Spongoserrula semicircularis* n. sp., holotype, x 180, rep.-no. KOMO 1994 IV-43.

Figs. 4, 10, *Falcispongus transitus transitus* n. sp.; Fig. 4: x 200, rep.-no. KOMO 1994 IV-6; Fig. 10: x 200, rep.-no.
13, 14: KOMO 1994 IV-7; Fig. 13: holotype, x 170, rep.-no. KOMO 1994 IV-5; Fig. 14: x 180, rep.-no. KOMO 1994 IV-9.

Figs. 6, 9, 11, *Gibberospongus spinosus* n. sp.; Fig. 6: x 200, rep.-no. KOMO 1994 IV-13; Fig. 9: holotype, x 180, rep.
12, 16, 18: no. KOMO 1994 IV-12; Fig. 11: x 200, rep.-no. KOMO 1994 IV-14; Fig. 12: x 200, rep.-no. KOMO 1994 IV-15; Fig. 16: x 180, rep.-no. KOMO 1994 IV-16; Fig. 18: x 180, rep.-no. KOMO 1994 IV-42.

Fig. 7: *Spongoserrula nuda* n. sp., holotype, x 150, rep.-no. KOMO 1994 IV-31.

Fig. 8: *Gibberospongus bispinosus* n. sp., holotype, x 170, rep.-no. KOMO 1994 IV-19.

Fig. 15: *Scutispongus sagittaeformis* n. sp., x 180, rep.-no. KOMO 1994 IV-134.

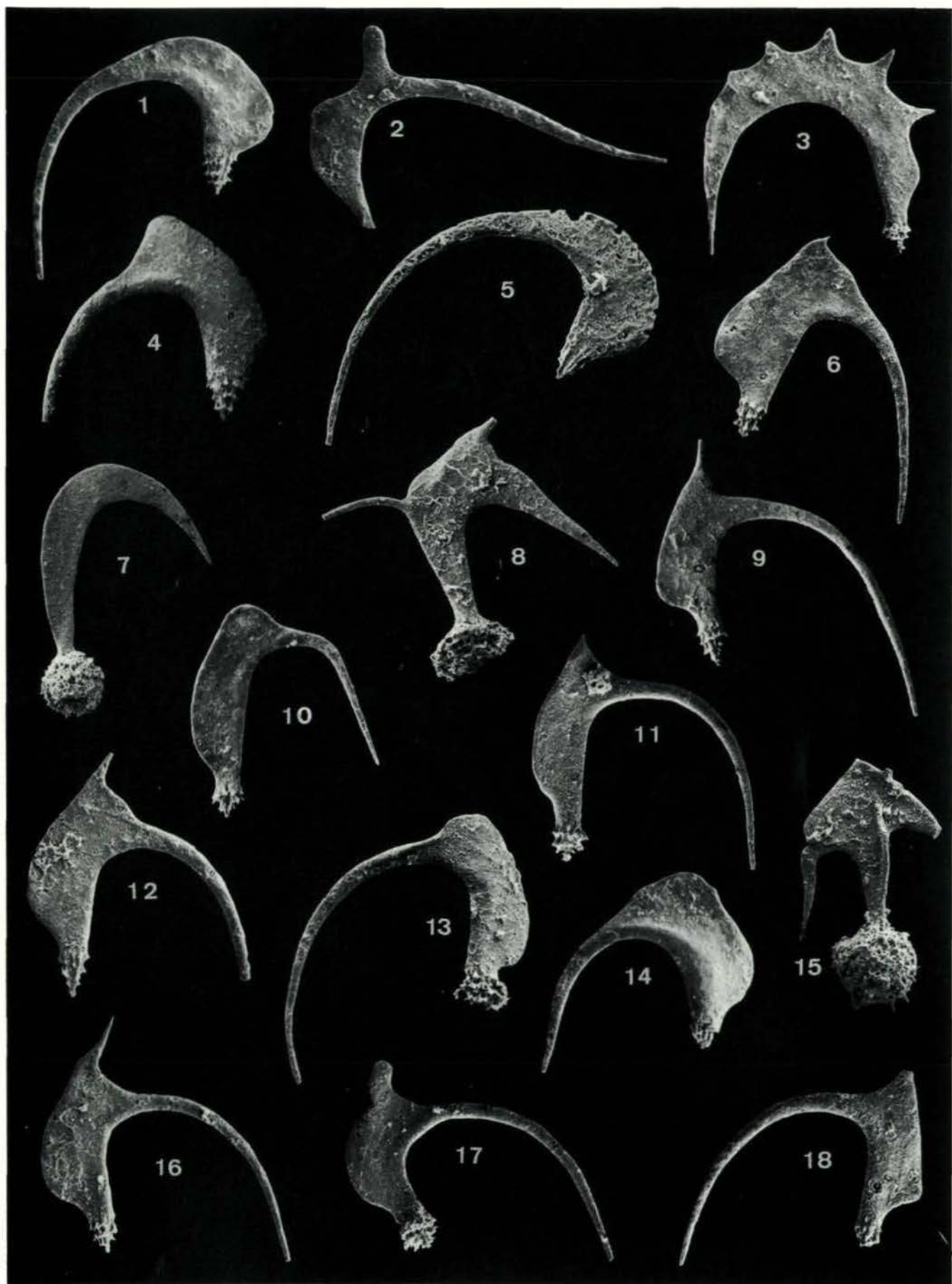Fig. 17: *Gibberospongus kraineri* n. sp., holotype, x 180, rep.-no. KOMO 1994 IV-2.
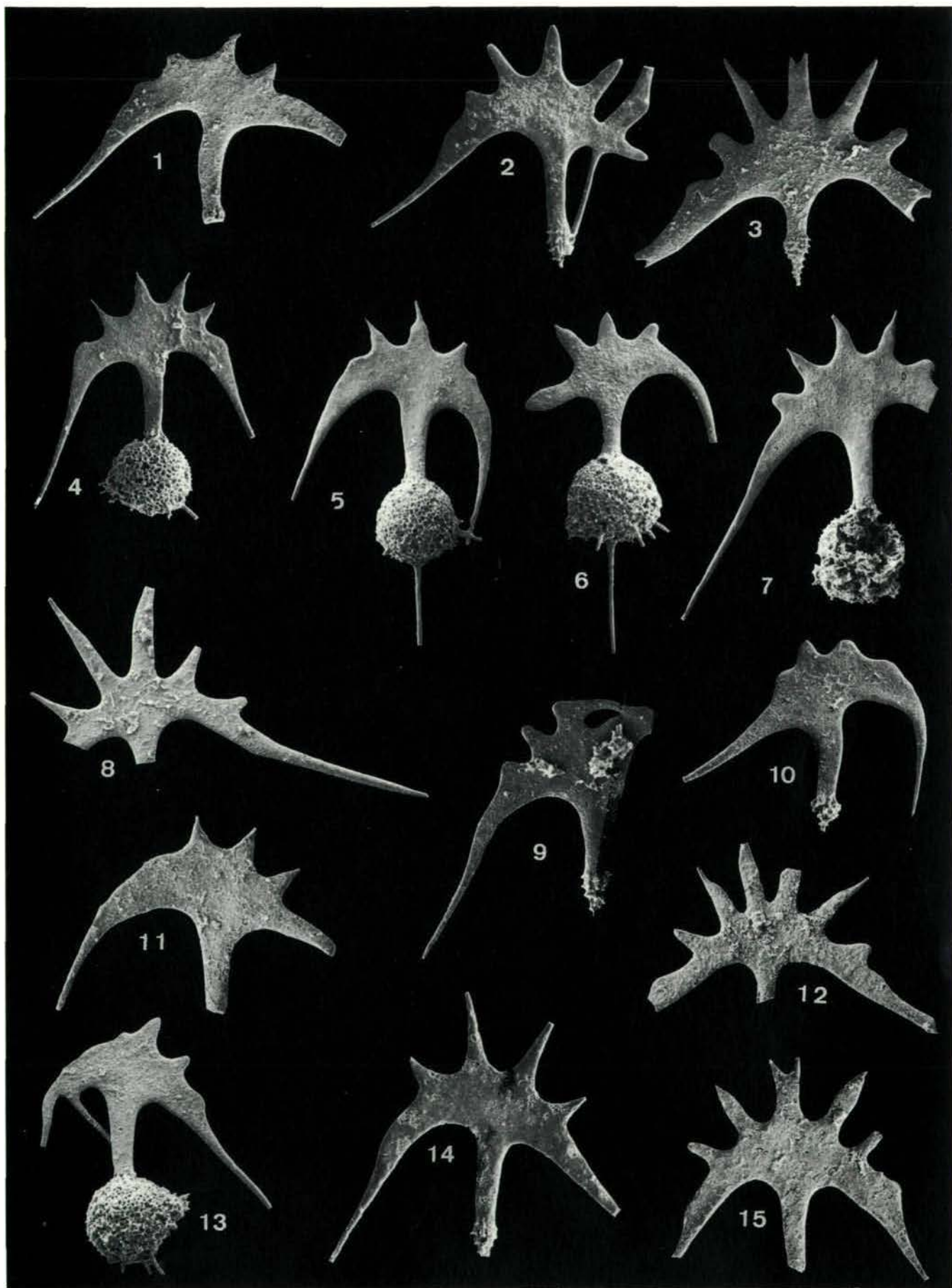
Plate 10

Plate 11

Fig. 1:   *Steigerispongus latofoliatus* n. sp., holotype, x 160, rep.-no. KOMO 1994 IV-77.

Fig. 2:   *Steigerispongus* cf. *asymmetricus* n. sp. with two spines on the secondary blade, x 150, rep.-no. KOMO 1994 IV-69.

Figs. 4, 5, 7:   *Steigerispongus asymmetricus asymmetricus* n. subsp.; Fig. 4: holotype, x 170, rep.-no. KOMO 1994 IV-67; Fig. 5: x 180, rep.-no. KOMO 1994 IV-70; Fig. 7: x 160, rep.-no. KOMO 1994 IV-71.

Fig. 3:   *Steigerispongus asymmetricus triangulodentatus* n. subsp., holotype, x 200, rep.-no. KOMO 1994 IV-72.

Fig. 6:   *Steigerispongus asymmetricus rectangularis* n. subsp., holotype, x 160, rep.-no. KOMO 1994 IV-73.

Fig. 8:   *Steigerispongus* cf. *asymmetricus asymmetricus* n. subsp., x 180, rep.-no. KOMO 1994 IV-74.

Fig. 9:   *Scutispongus bituberosus* n. sp., holotype, x 130, rep.-no. KOMO 1994 IV-117.

Fig. 10:   *Steigerispongus* ? *curvispinus* n. sp., holotype, x 180, rep.-no. KOMO 1994 IV-64.

Fig. 11:   *Steigerispongus asymmetricus* subsp. indet., x 160, rep.-no. KOMO 1994 IV-75.

Fig. 12:   *Scutispongus latus* n. sp., pathologic form with two teminal spines at one wing, x 150, rep.-no. KOMO 1994 IV-118.

Fig. 13:   *Scutispongus cephalus* n. sp., holotype, x 180, rep.-no. KOMO 1994 IV-64.
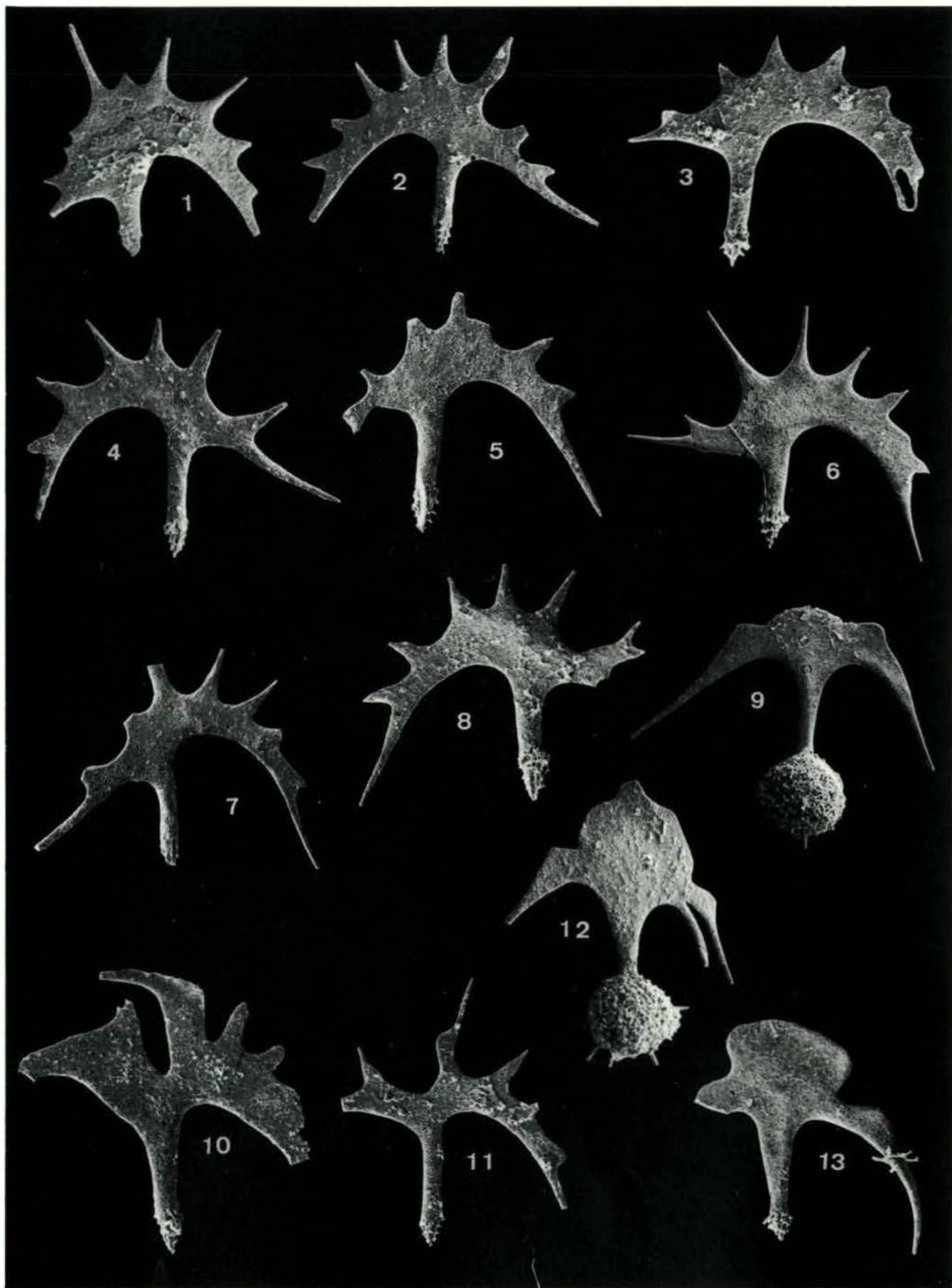
Plate 12

Fig. 1:   *Spongoserrula raridenticulata* n. sp., holotype, x , rep.-no. KOMO 1994 IV-141.

Fig. 2:   *Spongoserrula* cf. *rarauana trinodosa* n. subsp., x 150, rep.-no. KOMO 1994 IV-142.

Fig. 3:   *Spongoserrula rarauana trinodosa* n. subsp. x 130, rep.-no. KOMO 1994 IV-143.

Fig. 4:   *Spongoserrula bipolaris* n. sp., x 120, rep.-no. KOMO 1994 IV-144

Fig. 5:   *Spongoserrula bidentata* n. sp., x 170, rep.-no. KOMO 1994 IV-145.

Fig. 6:   *Gibberospongus* cf. *bispinosus* n. sp., pathologic form, x 150, rep.-no. KOMO 1994 IV-146.

Fig. 7:   *Scutispongus gackoensis* n. sp., holotype, x 150, rep.-no. KOMO 1994 IV-147.

Fig. 8:   *Scutispongus* aff. *S. reschi* n. sp., pathologic form (?), x 130, rep.-no. KOMO 1994 IV-148.

Fig. 9:   *Scutispongus cephalus* n. sp., holotype, x 130, rep.-no. KOMO 1994 IV-119.

Fig. 10:   *Scutispongus* cf. *sagittaeformis* n. sp., x 110, rep.-no. KOMO 1994 IV-150.

Fig. 11:   *Scutispongus gracilispinosus* n. sp., x 130, rep.-no. KOMO 1994 IV-151.

Fig. 12:   *Scutispongus bicornutus* n. sp., holotype, x 130 rep.-no. KOMO 1994 IV-152.

Figs. 13, 14:   *Steigerispongus dosztalyi* n. sp.; Fig. 13: holotype, x 130, rep.-no. KOMO 1994 IV-153; Fig. 14: x 170, rep.-no. KOMO 1994 IV-154.

Fig. 15:   *Gibberospongus spinosus* n. sp., x 130, rep.-no. KOMO 1994 IV-155.

Figs. 16–18:   *Steigerispongus subsymmetricus subsymmetricus* n. subsp.; Fig. 16: x 130, rep.-no. KOMO 1994 IV-156; Fig. 17: x 130, rep.-no. KOMO 1994 IV-157; Fig. 18: x 130, rep.-no. KOMO 1994 IV-158.
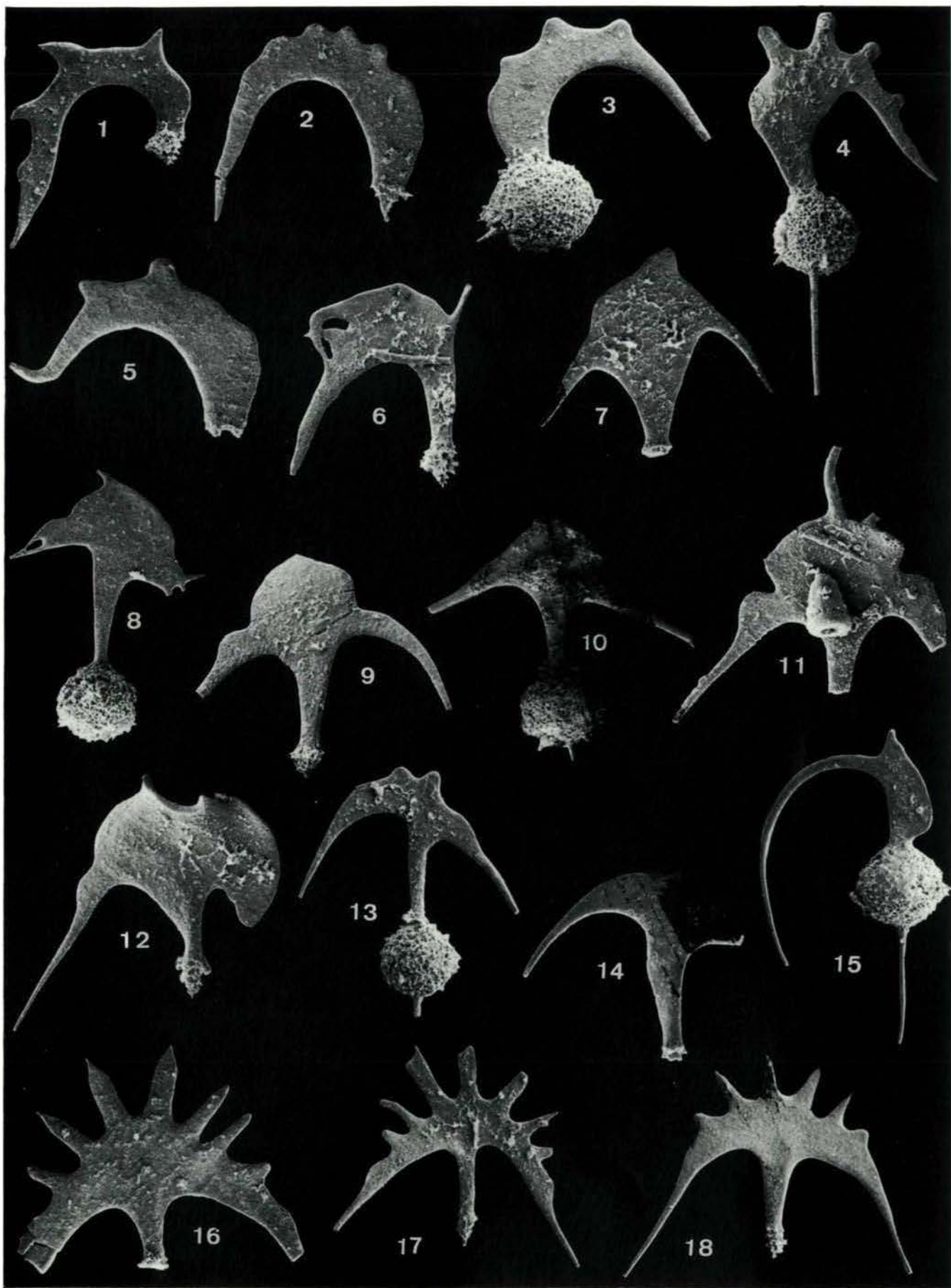
Plate 13

Fig. 1:   *Spongoserrula goricanae* n. sp., holotype, x 130, rep.-no. KOMO 1994 IV-159.

Fig. 2:   *Spongoserrula bifurcata parvispina* n. subsp., holotype, x 130, rep.-no. KOMO 1994 IV-160.

Fig. 3:   *Steigerispongus asymmetricus rectangularis* n. subsp., x 150, rep.-no. KOMO 1994 IV-161.

Fig. 4:   *Spongoserrula fluegeli fluegeli* n. subsp., x 120, rep.-no. KOMO 1994 IV-162

Fig. 5:   *Falcispongus transitus brevifoliaceus* n. subsp., x 200, rep.-no. KOMO 1994 IV-163.

Fig. 6:   *Scutispongus* ? *parvifoliatus parvifoliatus* n. subsp., holotype, x 200, rep.-no. KOMO 1994 IV-164.

Fig. 7:   *Steigerispongus asymmetricus asymmetricus* n. subsp., x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-165.

Fig. 8:   *Spongoserrula dehli* CORDEY et al., 1988, x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-166.

Fig. 9:   *Scutispopngus sagittaeformis* n. sp., holotype, x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-167.

Fig. 10:   *Scutispongus mocki* n. sp., holotype, x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-168.

Fig. 11:   *Steigerispongus* sp. C, x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-204.

Fig. 12:   *Bogdanella cordevolica* n. sp., holotype, x 130, sample RW 13, reddish late Cordevolian limestone, outcrop at the road about 500 m south of Pietra dei Saracini, Sosio Valley area, Sicily (Italy), rep.-no. KOMO 1994 IV-169.
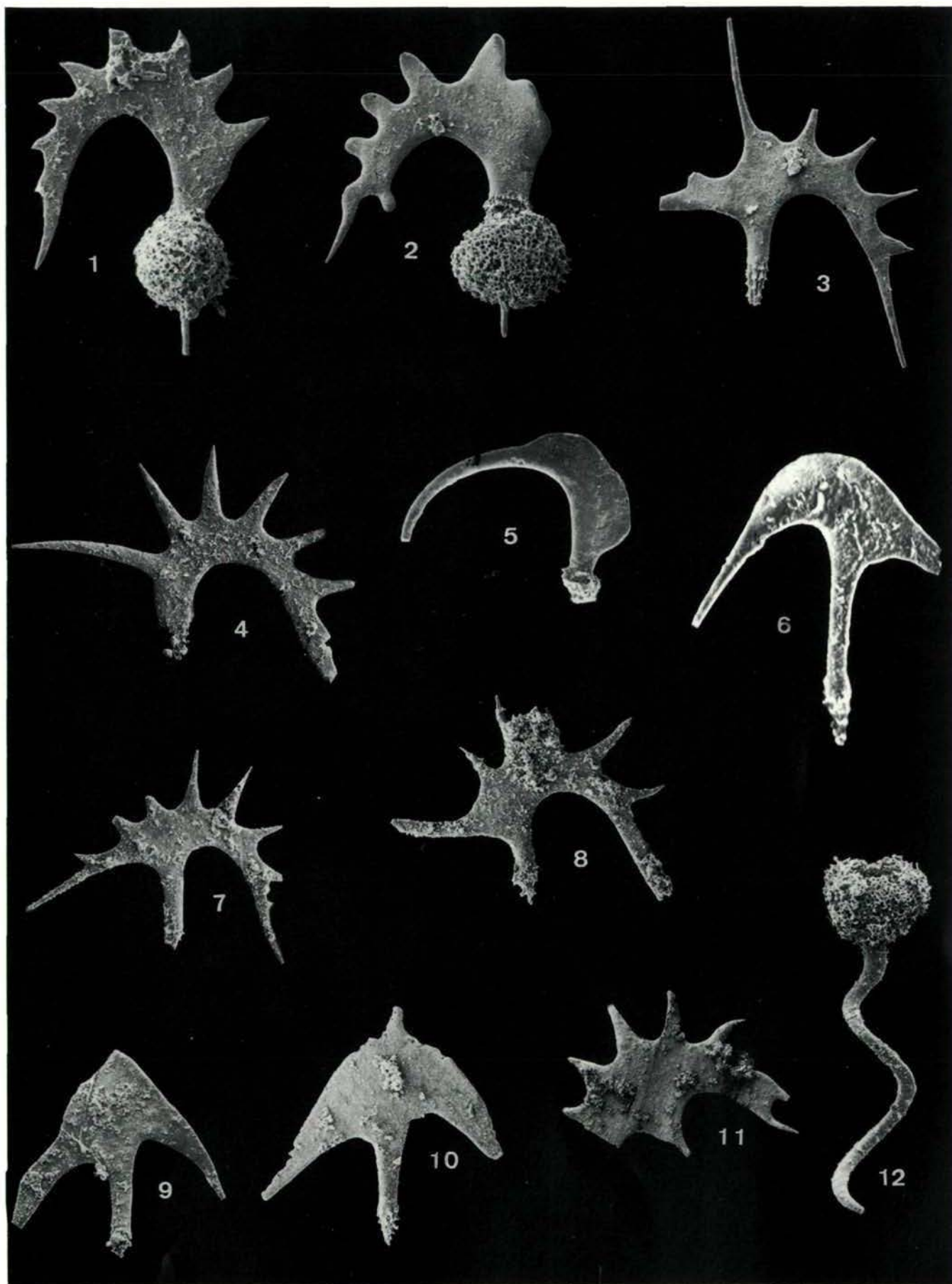
Plate 14

All figured specimens are from the middle part of Buchenstein Beds, sample St 1, at locality Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994). They belong to the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian).

Fig. 1:   *Falcispongus* cf. *hamatus* DUMITRICĂ, 1982, x 180, rep.-no. KOMO 1994 IV-170.

Figs 2, 3:   *Falcispongus hamatus* DUMITRICĂ, 1982; Fig. 2: x 150, rep.-no. KOMO 1994 IV-171; Fig. 3: x 150, rep.-no. KOMO 1994 IV-172.

Fig. 4:   *Falcispongus falciformis minor* n. subsp., holotype, x 180, rep.-no. KOMO 1994 IV-173.

Fig. 5:   *Falcispongus transitus brevifoliaceus* n. subsp., x 180, rep.-no. KOMO 1994 IV-174.

Figs. 6, 7:   *Spongoserrula antiqua* n. sp.; Fig. 6: holotype, x 150, rep.-no. KOMO 1994 IV-175; Fig. 7: x 150, rep.-no. KOMO 1994 IV-176.

Figs. 8, 9, 12: *Baumgartneria curvispina* DUMITRICĂ, 1982; Fig. 8: x 160, rep.-no. KOMO 1994 IV-177; Fig. 9: x 160, rep.-no. KOMO 1994 IV-178; Fig. 12: specimen with beginning development of a blade, x 150, rep.-no. KOMO 1994 IV-179.

Figs. 10, 11:   *Oertlispongus inaequispinosus* DUMITRICĂ, KOZUR & MOSTLER, 1980; Fig. 10: x 150, rep.-no. KOMO 1994 IV-180; Fig. 11: x 170, rep.-no. KOMO 1994 IV-181.

Figs. 13, 14:   *Pterospongus priscus priscus* n. subsp.; Fig. 13: x 150, rep.-no. KOMO 1994 IV-182; Fig. 14: holotype, x 170, rep.-no. KOMO 1994 IV-183.

Fig. 15:   *Scutispongus ? parvifoliatus primitivus* n. subsp., holotype, x 180, rep.-no. KOMO 1994 IV-205.

Fig. 16:   *Pterospongus parvifissus* n. sp., holotype, x 150, rep.-no. KOMO 1994 IV-184.

Figs. 17, 18:   *Pterospongus priscus tortilis* n. sp.; Fig. 17: x 170, rep.-no. KOMO 1994 IV-185; Fig. 18: holotype, x 150, rep.-no. KOMO 1994 IV-186.
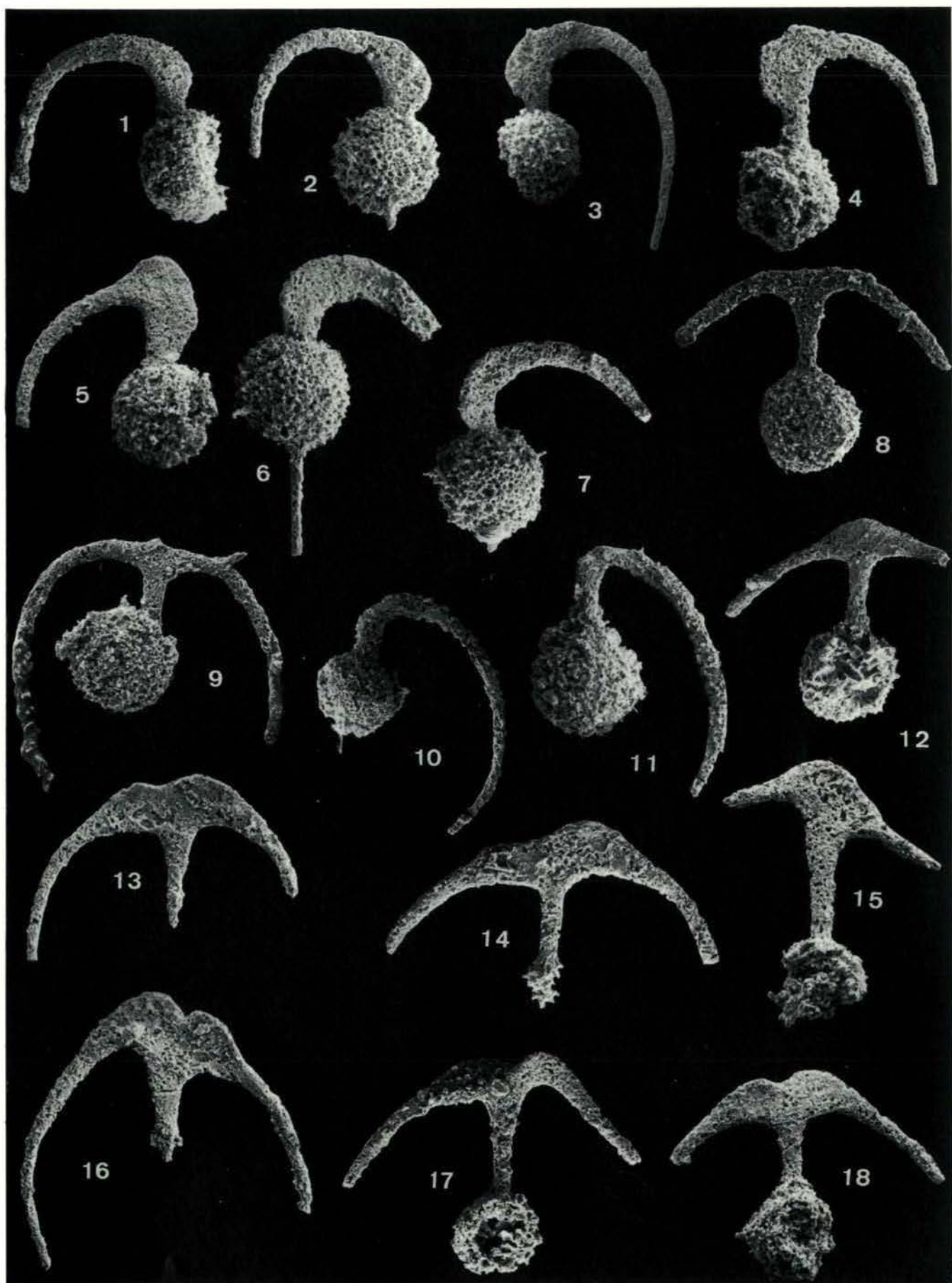
Plate 15

The specimens on Figs. 1-11, 13-15 are from the middle part of Buchenstein Beds, sample St 1, at locality Stinzesteig (Karawanken Mountains, southern Austria), locality and sample data see MOSTLER & KRAINER (1994). This sample belongs to the lower subzone (*Pterospongus priscus* Subzone) of *Muelleritortis cochleata* Zone (early middle Longobardian).

The specimens on Figs. 12, 16, 17 are from the uppermost Buchenstein Beds, 7 m below the Schlern Dolomite, sample Bi 1 of the section at the NE slope of Bielschitza Mt. about 1700 above sea level (Karawanken Mts., southern Austria), locality and sample data see MOSTLER & KRAINER (1994). This sample belongs to the middle subzone (*Spongoserrula rarauana* Subzone) of *Muelleritortis cochleata* Zone (middle Longobardian).

Fig. 1:   *Pterospongus alatus* DUMITRICĂ, 1982, x 180, rep.-no. KOMO 1994 IV-187.

Figs. 2,3:   *Pterospongus parvifissus* n. sp.; Fig. 2: holotype x 150, rep.-no. KOMO 1994 IV-188; Fig. 3: x 170, rep.-no. KOMO 1994 IV-189.

Figs. 4,5:   *Pterospongus altofissus* n. sp.; Fig. 4: x 150, rep.-no. KOMO 1994 IV-190; Fig. 5: holotype, x 120, rep.-no. KOMO 1994 IV-191.

Figs. 6,7,   *Scutispongus rostratus rostratus* (DUMITRICĂ, 1982); Fig. 6: x 150 rep.-no. KOMO 1994 IV-192; Fig. 7: x 150,
10, 12:   rep.-no. KOMO 1994 IV-193; Fig. 10: x 150, rep.-no. KOMO 1994 IV-194; Fig. 12: x 150, rep.-no. KOMO 1994 IV-195.

Fig. 8:   *Scutispongus rostratus incurvatus* n. subsp., holotype, x 200, rep.-no. KOMO 1994 IV-196.

Fig. 9:   *Scutispongus rostratus minutispinus* n. subsp., holotype, x 150, rep.-no. KOMO 1994 IV-197.

Fig. 11:   *Steigerispongus primus* n. sp., holotype, x , rep.-no. KOMO 1994 IV-198.

Figs. 13–15:   *Bogdanella praecursor* n. sp.; Fig. 13: holotype, x 150, rep.-no. KOMO 1994 IV-199; Fig. 14: x 170, rep.-no. KOMO 1994 IV-200; Fig. 15: x 150, rep.-no. KOMO 1994 IV-201.

Fig. 16:   *Spongoserrula rarauana rarauana* DUMITRICĂ, 1982, x 130, rep.-no. KOMO 1994 IV-202.

Fig. 17:   *Falcispongus* cf. *transitus* n. sp., x 150, rep.-no. KOMO 1994 IV-203.
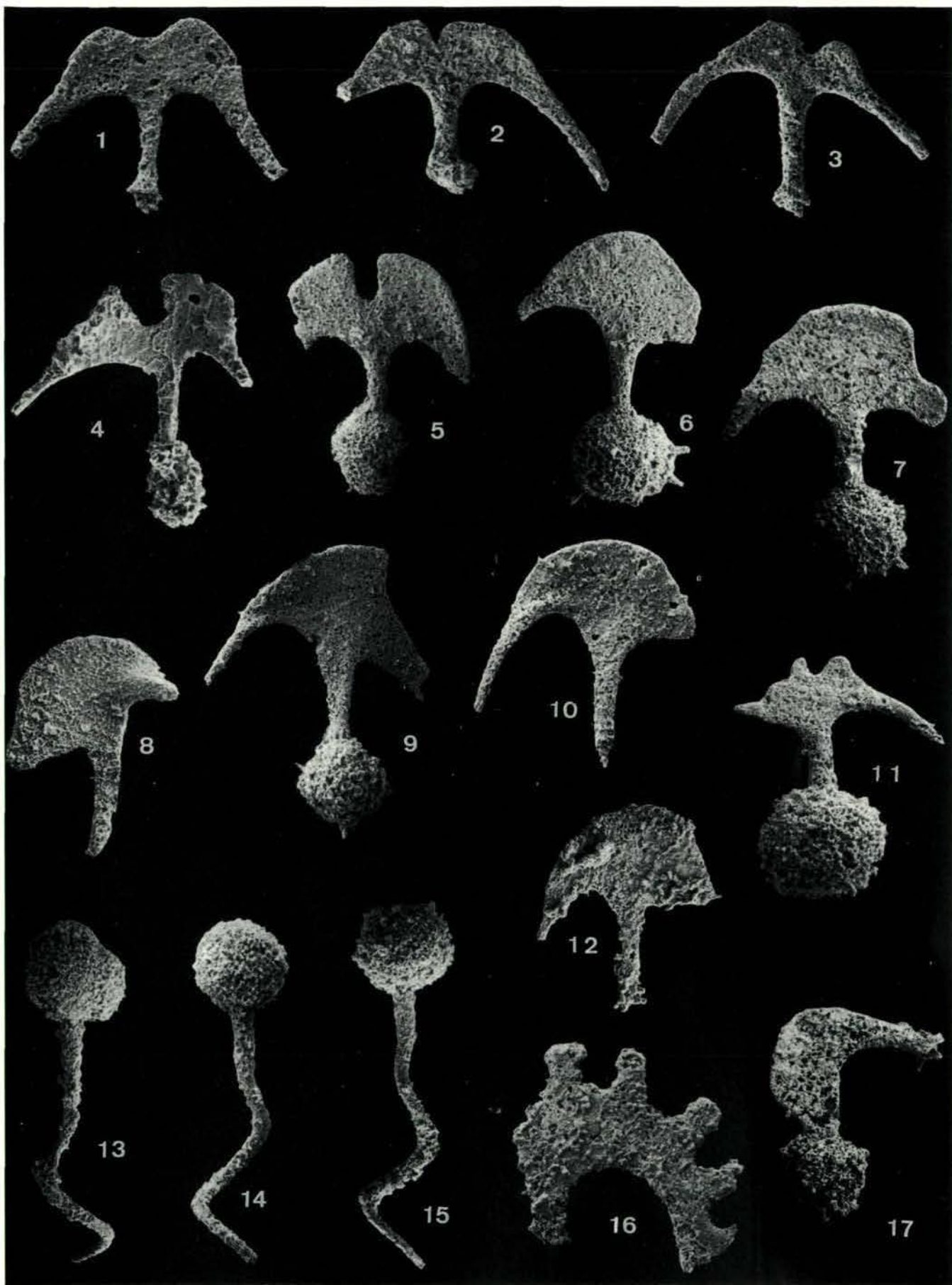
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RADIOLARIANS AND FACIES OF THE MIDDLE TRIASSIC
LOIBL FORMATION, SOUTH ALPINE KARAWANKEN MOUNTAINS
(CARINTHIA, AUSTRIA)

Heinz W. Kozur, Karl Krainer & Helfried Mostler

With 7 figures, 1 table and 13 plates

Abstract:
A geologic interpretation of the microfacies of Middle Triassic red pelagic limestones (Loibl Formation) of the South Alpine South Karawanken Mountains is given. The lowermost part of these limestones (Weiße Wand Member) contains a very rich radiolarian fauna. It has transitional character between the typical Illyrian radiolarian fauna of the upper *Paraceratites trinodosus* ammonoid zone and the typical Ladinian radiolarian fauna of the *Reitziites reitzi* ammonoid zone s.str. (defined by the first appearance of *Reitziites reitzi*), both well dated by ammonoids in the Felsőőrs section of the Balaton Highland (Hungary). Illyrian species clearly dominate, but first Ladinian species are subordinately present. Few species are restricted to this fauna. This association can be recognized also in the Balaton Highland (KOZUR & MOSTLER, 1994), in Slovenia (GORIČAN & RAMOVŠ, 1995), Japan (NAKASEKO & NISHIMURA, 1979) and in China (FENG, QINGLAI, 1992 and FENG, QINGLAI & LIU, BENPEI, 1993), in the two latter areas stratigraphically misinterpreted. The radiolarian fauna of the Weiße Wand Member defines the *Tiborella florida* Subzone of the *Spongosilicarmiger transitus* Zone and it is assigned to the uppermost Anisian (upper Illyrian), whereas, according to its conodont fauna, the largest part of the Loibl formation belongs to the Ladinian.
One new family, two new genera, 24 new species and two new subspecies are described.

Zusammenfassung:
Die Mikrofazies der mitteltriassischen roten pelagischen Kalke der Loibl Formation der südalpinen Südkarawanken wird beschrieben und geologisch interpretiert. Der unterste Teil dieser Kalke (Weiße-Wand-Member) enthält eine sehr reiche Radiolarienfauna. Sie hat Übergangscharakter zwischen der typisch illyrischen Radiolarienfauna der *Paraceratites trinodosus*-Ammonitenzone und der typisch ladinischen Radiolarienfauna der *Reitziites reitzi*-Ammonitenzone s.str. (Basis definiert mit dem ersten Einsetzen von *Reitziites reitzi*), die beide mit Ammoniten im Felsőőrs-Profil des Balaton-Hochlandes (Ungarn) gut definiert sind. Illyrische Arten dominieren bei weitem, aber erste ladinische Arten sind untergeordnet vorhanden. Wenige Arten sind auf diese Übergangsfauna beschränkt. Diese Radiolarien-Assoziation kann auch im Balaton-Hochland (KOZUR & MOSTLER, 1994), in Slowenien (RAMOVŠ & GORIČAN, 1995), in Japan (NAKASEKO & NISHIMURA, 1979) und in China (FENG, QINGLAI, 1992 und FENG, QINGLAI & LIU, BENPEI, 1993) nachgewiesen werden, wurde aber in den beiden letzteren Gebieten stratigraphisch fehlinterpretiert. Die Radiolarienfauna des Weiße-Wand-Members repräsentiert die *Tiborella florida*-Subzone der *Spongosilicarmiger transitus*-Zone. Sie wird in das obere Illyr (oberstes Anis) gestellt, während der größte Teil der Loibl-Formation nach der Conodontenfauna ins Ladin gehört.
Eine neue Familie, zwei neue Gattungen, 24 neue Arten und zwei neue Unterarten werden beschrieben

1. Introduction

The occurrence of red pelagic limestones in the South Alpine Triassic of the Karawanken Mountains was first mentioned by PREY (1973, 1975). From these limestones BAUER (1980) reported ammonites of Early Ladinian age from outcrops along the Zelenica forest road NW of the Loibltun-

nel in the central Karawanken Mountains. Despite a detailed sedimentological and stratigraphical analysis, these limestones have been compared and correlated with the Schreyeralm Limestone of the Northern Calcareous Alps and dated as Late Anisian - Early Ladinian (BAUER 1980, 1984).

KRAINER & MOSTLER (1992) introduced the term Loibl Formation for these red and grey lime-
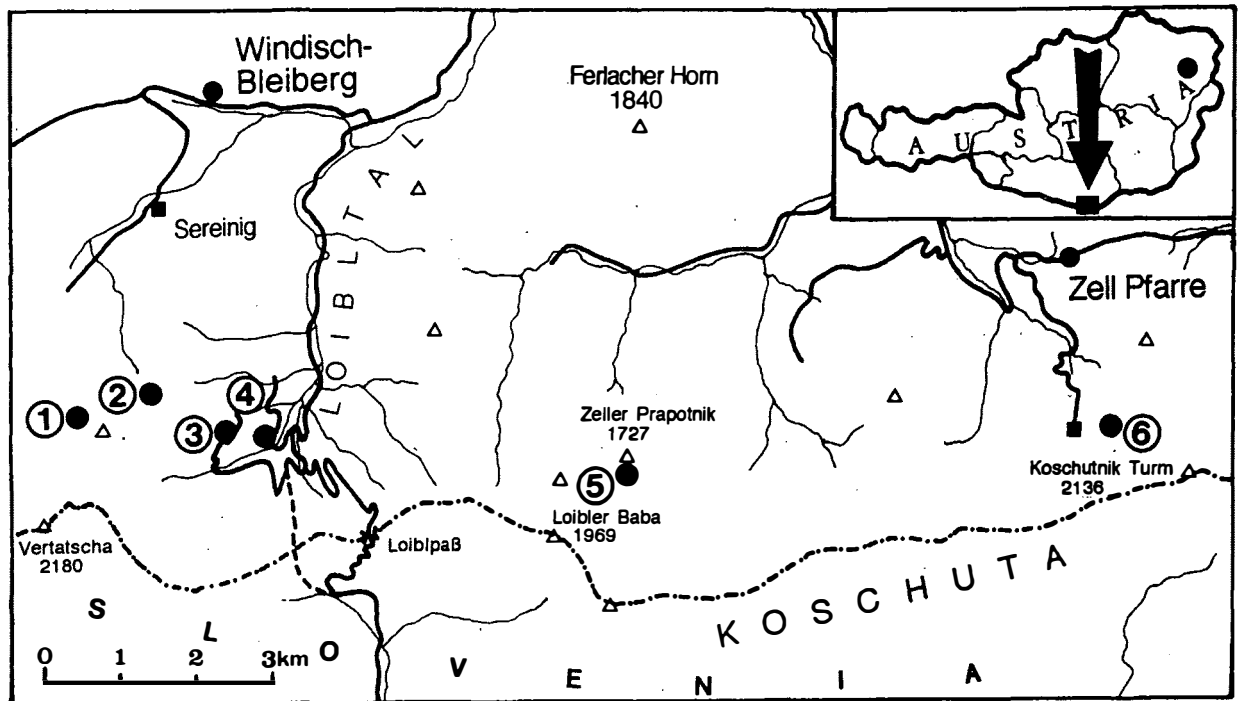
Fig. 1: Location map of investigated sections and outcrops.
1 = Weiße Wand, 2 = Heilige Wand, 3 = Selenitza forest road, 4 = Selenischniak, 5 = Zeller Prapotnik, 6 = Grosalm.

stones, which occur on top of massive, light grey *Tubiphytes-Archaeolithoporella*-limestones (Contrin Formation). Two types of limestones can be distinguished in the Loibl Formation: (a) thin nodular limestones, known from only one locality at the Weiße Wand (Weiße Wand Member), and (b) massive to indistinctly bedded, partly nodular limestones (Selenischniak Member).

KRAINER & MOSTLER (1992) gave a detailed description of the Weiße Wand Member, which has been dated as Early Fassanian based on conodonts and radiolarians (*Spongosilicarmiger transitus* Subzone of the *Spongosilicarmiger italicus* Zone s.l.). KOZUR et al. (1994) assigned the conodont fauna of the Weiße Wand Member in the uppermost Illyrian. Subsequently, KOZUR (1995) elevated the *S. transitus* Subzone to zonal rank and correlated it with the *Kellnerites felsoeoersensis* ammonoid zone that he assigned to the latest Illyrian immediately below the *Reitziites reitzi* Zone s.str. (lower boundary defined with the first appearance of *Reitziites* reitzi) of Early Ladinian age. Thus, the conodont and radiolarian faunas give the same latest Illyrian age for the Weiße

Wand Member, whereas the Selenischniak Member displays Ladinian age.

The aim of the present paper is to characterize the limestones of the Loibl Formation, particularly of the Selenischniak Member in terms of regional distribution, facies, microfacies, microfauna (radiolarians of the Weiße Wand Member), to discuss the depositional environment and stratigraphic range of the Loibl Formation, and to describe the rich radiolarian fauna of the Weiße Wand Member, the richest radiolarian fauna of the *Tiborella florida* Subzone of the *Spongosilicarmiger transitus* Zone that is known so far.

2. Location of the investigated outcrops of the Loibl Formation

Pelagic limestones of the Loibl Formation are exposed in the central part of the southern Karawanken Mountains in southern Carinthia (Austria), which belong to the Southern Alps, and are separated from the Northern Karawan-

ken Mountains (Eastern Alps) by the Periadriatic Line.

The easternmost occurrence is a small outcrop at the Grosalm east of the Koschutahaus, the westernmost outcrop lies at the Weiße Wand south of the Märchenwiese. Outcrops studied in the present paper are located (1) at the Weiße Wand, (2) at the Heilige Wand, (3) along the Zelenica forest road, (4) near Selenischniak, (5) at the Zeller Prapotnik and (6) Grosalm. All locations are shown in Fig. 1.

3. Previous work and geologic setting

The first investigations of the Triassic sequence in the Karawanken Mountains date back to the last century (e.g. MOJSISOVICS, 1871, TELLER 1887, 1898), but until now little was known on the facies and stratigraphy of the Triassic, particularly the Middle Triassic sequence. TELLER (1898) already pointed out that the Triassic of the Southern Karawanken Mountains differs significantly from the Triassic of the Northern Karawanken Mountains, which are part of the Eastern Alps (Lician Drau Range). According to BAUER (1973, 1980, 1984) and BAUER et al. (1983), the Periadriatic Line, which separates these two tectonic units of the Southern and Northern Karawanken Mountains, does not represent a facies boundary concerning the Triassic of the two units.

After BAUER (1980) and BAUER et al. (1983), the Middle Triassic of the Southern Karawanken Mountains is composed of the "Alpine Muschelkalk" (Anisian), overlain by "Bankkalke, Hornsteinkalke und Mergel" (Late Anisian – Ladinian), volcanic rocks, red and grey limestones (Schreyeralmkalk; Late Anisian – Ladinian) and Schlerndolomite (see also geological map of BAUER, 1985).

This stratigraphic scheme differs from the results of our investigations, which showed that the Middle Triassic of the Southern Karawanken Mountains displays a typical South Alpine character (Fig. 2, see KOZUR et al., 1994, MOSTLER & KRAINER 1994). The Middle Triassic begins with
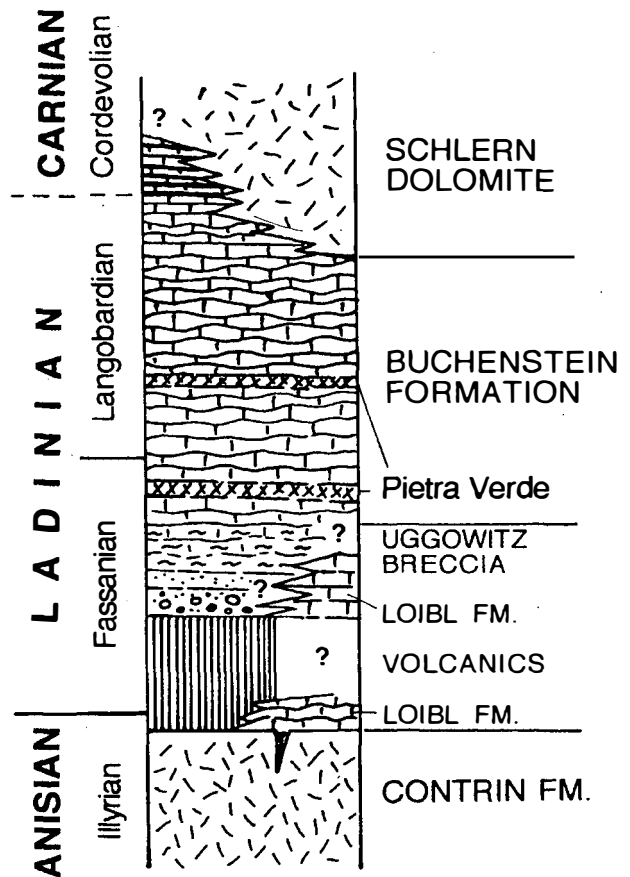
Fig. 2: Stratigraphy of the South Alpine Middle Triassic sequence in the central Karawanken Mountains (modified after KOZUR et al., 1994).

several hundred meters thick, well-bedded and partly evaporitic platform carbonates that are regarded as an equivalent of the Lower Sarl Formation of the Dolomites. They are overlain by dark grey, well-bedded and bioturbated marly limestones ("Wurstelkalke"), thin bedded, laminated dolomites and locally several meter-thick red marls with intercalated grey limestone beds. These red marls probably represent an equivalent of the Lower Peres Formation of the Dolomites. Laminated dolomites and red marls are overlain by massive, light grey platform carbonates of the Contrin Formation.

In the central Karawanken Mountains pelagic limestones of the Loibl Formation overlap the shallow water carbonates of the Contrin Formation; the boundary between both formations is very sharp. The Loibl Formation is a few meters to a

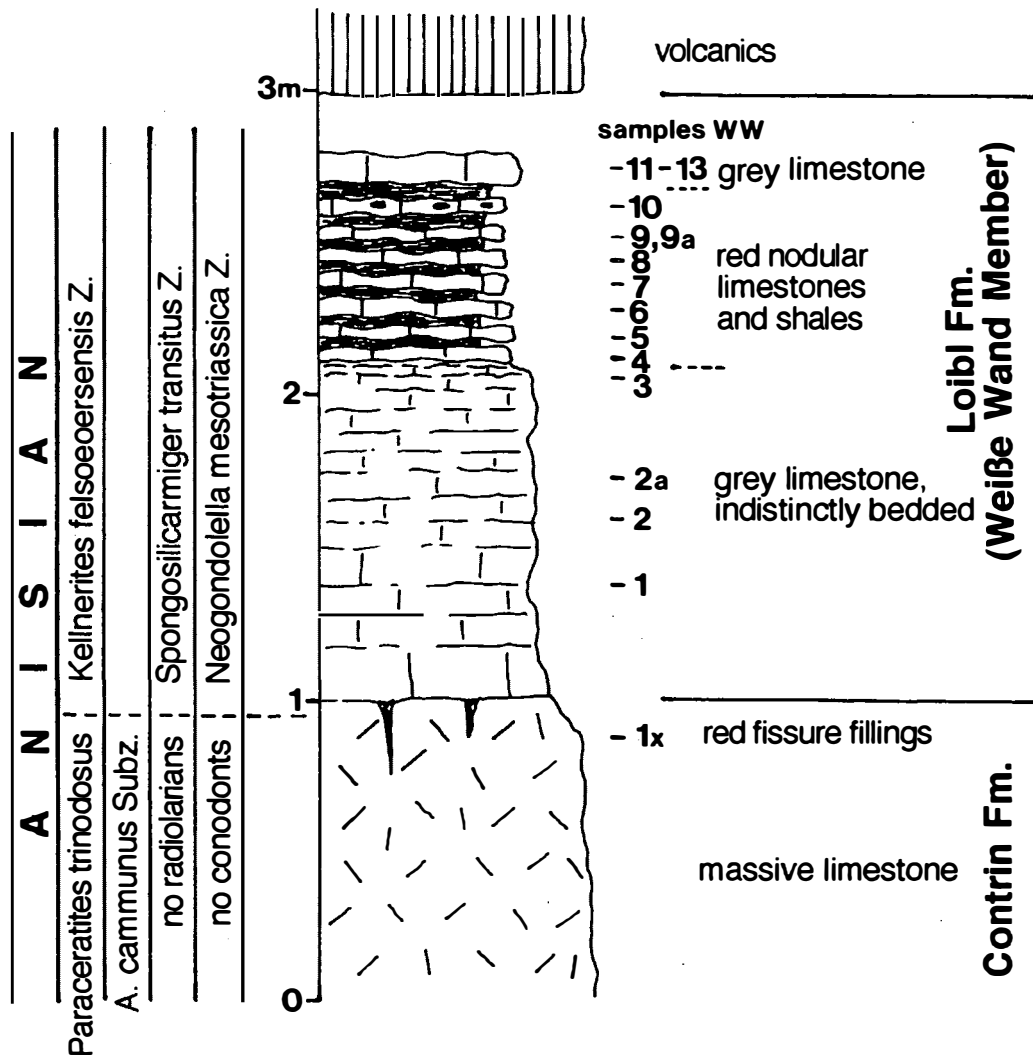**Fig. 3:** Measured section through the Loibl Formation (Weiße Wand Member) at the Weiße Wand (modified after KRAINER & MOSTLER, 1992). Location see Fig. 1.

few tens of meters thick. It interfingers with and is overlain by volcanic rocks of andesitic to dacitic composition with a maximum thickness of about 100 m (OBENHOLZNER, 1985). Agglomerates at the base of the volcanic sequence contain a few red limestone clasts that were derived from the Loibl Formation, definitely demonstrating that parts of the Loibl Formation are older than the volcanic rocks. This is also proven in the Weiße Wand section, where volcanic rocks overlay the Weiße Wand Member of the Loibl Formation (Fig. 3). On the other hand, the middle part of the Selenischniak Member at Zelenitza forest road contains thin tuff layers and altered volcanic rock fragments in-

dicating that a part of the volcanism is older than this level (Fig. 2).

The volcanic rocks are overlain by polymict conglomerates and sandstones, which are an equivalent of the Uggowitz Breccia and not part of the "Alpine Muschelkalk" as proposed by BAUER (1980, 1985) and BAUER et al. (1983). The Uggowitz Breccia contains also reworked limestone clasts that were derived from the Loibl Formation, and abundant volcanic clasts from the underlying volcanic rocks.

The conglomerates and sandstones of the Uggowitz Breccia grade upward into marls and marly limestones, which are overlain by evenly bedded

and nodular cherty limestones and intercalated greenish tuffs (Pietra Verde) of the Buchenstein Formation. Conodonts and radiolarians from the Buchenstein Formation indicate Late Fassanian to Late Langobardian age (KOZUR et al. 1994, MOSTLER & KRAINER 1994).

Middle Triassic red pelagic limestones of the Southern Karawanken Mountains occur in two different stratigraphic horizons: (1) In the Loibl Formation (KRAINER & MOSTLER 1992) above massive, light grey, shallow water platform carbonates of the Contrin Formation, and (2) within the Buchenstein Formation.

Pelagic limestones of the Loibl Formation are exposed in the central Karawanken Mountains between the Grosalm and Weiße Wand, where the interfingering and overlying volcanic rocks reach their greatest thickness.

Two different types of limestones can be distinguished for which two members are discriminated:

(a) Weiße Wand Member

A thin sequence of grey and red, partly cherty nodular limestones with thin marl intercalations. The limestones consist of wackestones rich in radiolarians and sponge spiculae. The sequence is exposed at the Weiße Wand, where it sharply overlays massive limestones of the Contrin Formation and is overlain by volcanic rocks.

The conodont fauna of the Weiße Wand Member was derived from a fissure filling of red pelagic limestones of the Weiße Wand Member in the underlying platform carbonates (Contrin Formation). It contains *Neogondolella balkanica* BUDUROV & STEFANOV, *Nicoraella kockeli* (TATGE), *Paragondolella* ? *pridaensis posteroacuta* KOZUR, KRAINER & MOSTLER, *Paragondolella* n. sp. ex gr. *excelsa* MOSHER and indicates latest Illyrian age. It corresponds to the conodont fauna of the same age (*Neogondolella mesotriassica* Zone or the contemporaneous *Paragondolella* ? *trammeri praetrammeri* Zone for the open sea pelagic facies) from Šmarna Gora near Lubljana, Slovenia (RAMOVŠ & GORIČAN, 1995).

(b) Selenischniak Member

It consists of massive to indistinctly thick bedded red and grey limestones with a total thickness of a few tens of meters. Due to strong tectonic overprinting complete sections are not preserved. In the strongly disturbed section exposed along the Zelenica forest road, thin nodular limestones and decimetre thick tuffs are intercalated. The Selenischniak Member overlays also the Contrin Formation. Overlying volcanic rocks are not exposed.

The conodont fauna that was derived from limestones of the Selenischniak Member of the Loibl Formation contains *Paragondolella trammeri*, *P. alpina*, advanced *P. excelsa*, *Neogondolella cornuta ladinica*, *N. mesotriassica*, *N. longa*, *N. balkanica*, and in the upper part already primitive *Budurovignathus*. It indicates early to late Fassanian age.

Best outcrops of the Selenischniak Member are located along the Selenitza forest road, along the road to the locality Selenischniak, and at the Zeller Prapotnik.

Locality Selenitza forest road (Fig. 4)

This forest road leads from Pamschbauer to the Selenitza Graben, the outcrops are located along the road at an altitude of 1120–1130 m (see BAUER, 1985, Geol. Karte der Westkarawanken).

The sequence is tectonically overprinted and strongly disturbed, the exposed thickness measures about 30 m. From base to top the sequence is composed of the following intervals:

(a) 12 m indistinctly thick bedded grey limestones with thin reddish nodular limestones intercalations.

(b) 10 m evenly bedded and nodular red limestones (10 m) with four intercalated tuff layers. The red limestones contain crinoid fragments and rarely ammonites.

(c) 6 m indistinctly bedded grey limestones with an intercalated thin conglomerate layer.

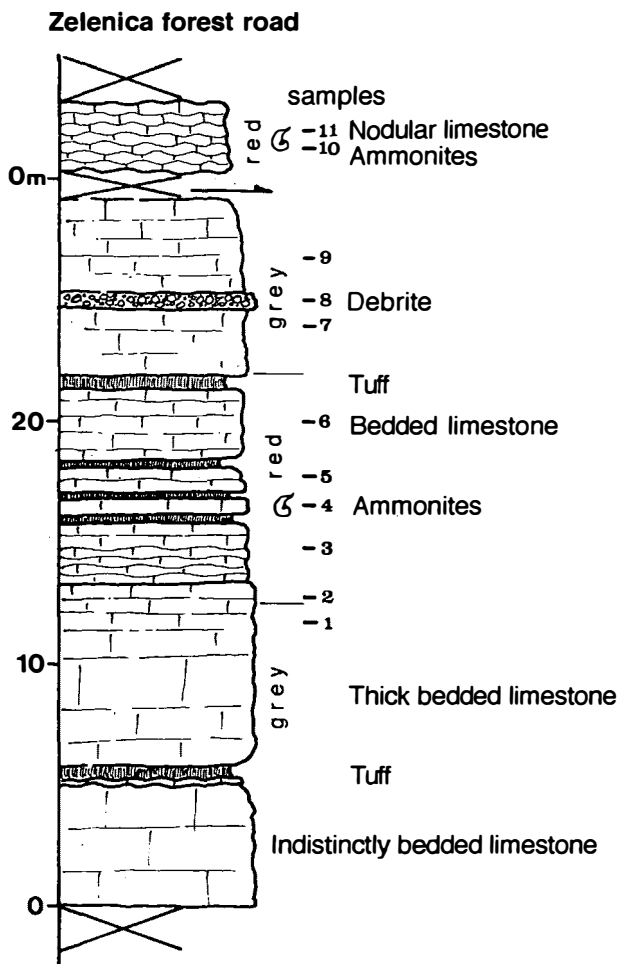(d) 3 m red nodular limestones with ammonites on top of the sequence (Pl. 12, Fig. 1).

Zelenica forest road

Fig. 4: Measured section through limestones of the Loibl Formation exposed along the Selenitza forest road. Location see Fig. 1.

Microfacies of interval a: The grey limestones are composed of laminated, locally bioturbated bioclastic wackestones with radiolarians, sponge spiculae and shell fragments being the most abundant bioclastic constituents. Subordinate are echinoderm fragments, foraminifers, gastropods and ostracods. The groundmass is composed of micrite. Up to a few cm large red and grey micritic intraclasts are sparsely distributed in this facies. These intraclasts contain less bioclasts (radiolarians, filaments, echinoderms, sponge spiculae, foraminifers and ostracods) than the surrounding rock. The intraclasts frequently display stylolithic grain contacts.

Microfacies of interval b: The red limestones consist of bioclastic wackestones/packstones and

bioclastic grainstones. The bioclastic wackestones appear massive and contain echinoderms, radiolarians, sponge spiculae, shell fragments, foraminifers and ammonites. The crinoid fragments have a diameter up to 1 cm, some of them show borings. Three types of lithoclasts have been recognized: small, grey micritic clasts with algae and *Tubiphytes*, derived from shallow water environments, red micritic intraclasts with diameters up to 1 cm, and altered volcanic rock fragments (Pl. 12, Figs. 3 and 4).

The bioclastic grainstones/packstones contain abundant echinoderm and shell fragments, which are densely packed and cemented by calcite spar. Microstylolites indicate pressure solution. Small patches of micritic to microsparitic groundmass are present. The echinoderm fragments frequently display syntaxial overgrowths. Shell fragments are almost completely recrystallized. A few micritic lithoclasts containing radiolarians have been observed.

Microfacies of interval c: The grey limestone interval consists of bioclastic wackestones/packstones, which contain shell fragments, echinoderm fragments, ostracods, foraminifers, calcisponges, micritic algae and *Tubiphytes*. Some of the bioclasts are derived from shallow water environments. The groundmass consists of micrite and small patches of sparite. Locally the bioclasts display micritic envelopes. In some samples peloids and small intraclasts are present.

The intercalated conglomerate bed is 30 cm thick, poorly sorted and grain supported, and consists of angular to subangular clasts with stylolithic grain contacts and micritic groundmass (Pl. 12, Fig. 6). The following clast types have been recognized:
- Bioclastic wackestones with radiolarians, spiculae and echinoderms.
- Bioclastic wackestones, rich in echinoderms and shell fragments and a few micritic intraclasts.
- Shallow-water limestone clasts (grainstones).
- Bioclasts (crinoid fragments).
- Altered volcanic rock fragments.

Microfacies of interval d: The red nodular limestones on top of the sequence are composed of

bioturbated wackestones. The most frequent bioclasts are radiolarians, sponge spiculae and filaments. Subordinate are echinoderms, foraminifers, gastropods and ammonite fragments. A few micritic grey intraclasts are present too. This facies is very similar to the red nodular limestones of the Weiße Wand Member (see KRAINER & MOSTLER, 1992).

Locality Selenischniak

Along the road to Selenischniak, NW of the bridge crossing the Zelenitza Graben, tectonically disturbed grey, red and beige limestones of the Selenischniak Member are exposed. The limestones are bedded (10 - 40 cm), nodular and indistinctly bedded to massive. In the field crinoids, brachiopods and solitary corals have been observed in red and beige limestones. The limestones of this locality are composed of the following microfacies:
(a) Filament packstones (Pl. 13, Fig. 1).
(b) Wackestones/packstones rich in radiolarians, filaments and spiculae.
(c) Bioclastic wackestones/packstones containing lithoclasts.
(d) Wackestones with bioclasts derived from shallow water environments. This type contains segmented and unsegmented calcisponges, sphinctozoans and hexactinellid sponges (Pl. 13, Figs. 2, 3) as well as solitary corals, echinoderms, shell fragments, foraminifers, gastropods and ostracods. Some of the larger bioclasts are encrusted by *Tubiphytes*. The groundmass is composed of micrite and rarely of sparite. Locally peloids and individual, cm-large lithoclasts are present. Lithoclasts are composed of micrite and a few bioclasts. Some of the lithoclasts have been identified as reworked red micritic limestones containing filaments, spiculae and ostracods.

Locality Zeller Prapotnik

At the peak of the Zeller Prapotnik (1727 m) light grey, massive shallow water carbonates of the Contrin Formation are overlain by red limestones of the Loibl Formation. In the uppermost part of the Contrin Formation dm-thick and up to several m deep fissures filled with red limestones and tuffaceous material are developed. Breccias composed of grey limestone clasts embedded in red micritic matrix are exposed on top of the Contrin Formation. These breccias probably represent scarp fault breccias. The breccias and fissures developed during breakdown of the Contrin Platform.

A few meters south of the peak grey limestones of the Contrin Formation are overlain by a well developed hardground, which is superimposed by condensed red nodular limestones with an exposed thickness of 50 cm. The red limestones frequently contain crinoid fragments, rarely ammonites. BAUER (1984) reported the occurrence of *Kellnerites* sp. These red nodular limestones probably belong to the Weiße Wand Member.

The grey limestones of the Contrin Formation are composed of the following microfacies:

(a) Algal-Tubiphytes bindstones
Algae and *Tubiphytes* form a framework with pore space filled in part with pelmicritic matrix, in part with calcite spar. Other bioclasts are shell fragments, gastropods, echinoderms, foraminifers and individual bryozoan fragments. Some bioclasts display a micritic envelope, some are encrusted by *Tubiphytes*.

(b) Bioclastic grainstone
These limestones are indistinctly laminated, poorly to moderately sorted and contain echinoderm fragments, shell fragments and foraminifers. Bioclasts are frequently encrusted by micritic algae and *Tubiphytes*. Peloids are a common lithoclast type.

(c) Bioclastic wackestones/packstones
These rocks contain shell fragments, echinoderms, foraminifers, gastropods, algae (partly dasycladaceans), *Tubiphytes* and *Olangocoelia*. Many bioclasts are incrusted by algae and *Tubiphytes*. These wackestones/packstones are relatively densely packed, the matrix consists of micrite.

In the overlying red limestones of the Loibl Formation the following microfacies have been recognized:

(a) Bioclastic packstone, locally bioturbated, with abundant radiolarians and filaments, and a few echinoderms, sponge spiculae, foraminifers, gastropods and ostracods in a micritic matrix. Rarely small voids filled with calcite spar or siltite are present (Pl. 13, Fig. 5).

(b) Bioclastic wackestone/packstone containing abundant echinoderm fragments, particularly crinoid ossicles up to 1 cm in diameter, some being impregnated with Fe-hydroxids and/or showing borings. Other bioclasts are shell fragments, brachiopods, gastropods foraminifers and ammonites. Angular grey clasts from shallow water carbonates and volcanic rock fragments are present. The matrix is composed of micrite.

(c) Bioclastic wackestone containing abundant angular lithoclasts that were derived from shallow water carbonates containing *Tubiphytes* (reworked Contrin Limestone). Rarely red limestone clasts with radiolarians (reworked limestones of the Loibl Formation) are also present. Bioclasts are filaments, echinoderms and poorly preserved fragments of ? radiolarians (Pl. 13, fig. 6).

Intercalated beige limestones consist of bioclastic wackestones, which contain segmented and unsegmented calcisponges, and subordinate hexactinellid sponges in a micritic matrix. Shell fragments, foraminifers, ostracods and individual red micritic intraclasts are present, too.

4. Interpretation of the microfacies data

Fissure fillings in the uppermost Contrin Formation (Weiße Wand, Heilige Wand, Zeller Prapotnik) and breccias indicate rapid breakdown and drowning of the Contrin carbonate platform. Red and grey limestones of the Loibl Formation composed of wackestones rich in radiolarians, sponge spicules and filaments represent pelagic deposits formed by fallout from suspension. Siliceous sponges in red nodular limestones of the Weiße Wand Member represent an autochthonous soft-ground fauna of an aphotic pelagic environment with water depths around 200 m (KRAINER & MOSTLER 1992). A pelagic environment is also indicated by a hardground and condensed nodular limestones at the Zeller Prapotnik, pointing to very low sedimentation rates, an by the conodont and radiolarian faunas. Intercalated are hemipelagic sediments containing platform derived detritus (bioclasts and lithoclasts) mixed with autochthonous sediment.

The conglomerate bed, which is intercalated in grey limestones of the Loibl Formation exposed along the Zelenitza forest road, is interpreted as a submarine debris flow. Intercalated tuff layers point to volcanic activity during sedimentation of the Loibl Formation. This is also indicated by the volcanics overlying the uppermost Illyrian Weiße Wand Member and by clasts of altered volcanics in the Lower Ladinian Selenischniak Member. Volcanic activity seems to be related to the breakdown of the carbonate platform and formation of small intraplatform basins.

The facies of the Loibl Formation, composed of a thin sequence of pelagic and hemipelagic sedimentary rocks with a thin intercalated debris flow may have been deposited in a transitional distal slope to basin environment.

5. Comparison of Middle Triassic red pelagic limestones of the Southern and Northern Alps

In the Middle Triassic of the Southern Alps red pelagic limestones occur in the following stratigraphic levels:

(1) ASSERETO (1971) described a 10–20 m thick sequence of red and grey marls and tuffaceous marls with intercalated thin nodular dolomitic limestones (*Trinodosus* layer auct. pro parte). This sequence, exposed in the southeastern Dolomites near Dont on top of the Dont limestone, has been named the Mte. Bivera Formation (PISA 1972, PISA et al., 1980). From the Mte. Bivera Formation FARABEGOLI et al. (1984) described five subenvi-

ronments, and dated the sequence as Illyrian (*Trinodosus* Zone) based on ammonites and conodonts.

(2) In the Recoaro area red pelagic cherty limestones occur in the Buchenstein beds of Early Ladinian age.

(3) The third stratigraphic level containing red pelagic limestones is the Longobardian part of the Buchenstein Formation ("Roter Cephalopodenkalk", "Clapsavon Limestone"). These red, ammonite-bearing limestones are up to 45 m thick. They have first been recognized by STUR (1856) and described by MOJSISOVICS (1880). From these limestones MOJSISOVICS (1882) and TOMMASI (1899) described a rich ammonite fauna. They also contain radiolarians, bivalves, gastropods and echinoderm fragments. They locally overlie dolomitic limestones of the Mte. Tiarfin. At their base locally thin slump breccias are developed (PISA, 1972).

As mentioned above, in the South Karawanken Mountains, red pelagic limestones occur in the same stratigraphic levels, in the Loibl Formation of latest Illyrian to late Fassanian age and in the Buchenstein Formation of late Fassanian to late Longobardian age.

From the Middle Triassic of the Northern Calcareous Alps two types of red limestones are known: Schusterbergkalk and Schreyeralmkalk.

The Schusterbergkalk occurs outside of the Hallstatt Zone, particularly in the southern part of the western Northern Calcareous Alps. The Schusterbergkalk is composed of variegated, mostly red cherty nodular limestones, overlying the Reifling Formation. In the Öfenbach section near Saalfelden (Salzburg) the Schusterbergkalk represents the uppermost 5 m of the Reifling Formation and is regarded to be a variety of the Reifling Formation and dated as Fassanian (TOLLMANN, 1976; KRAINER & STINGL, 1986) although according to SCHNETZER (1934) the Schusterbergkalk contains an Illyrian ammonite fauna.

The Schreyeralmkalk is 10–15 m thick and consists of red, thick bedded, extremely condensed micritic limestones. The Schreyeralmkalk is restricted to the Hallstatt Zone. It is, like the Schusterbergkalk, partly developed on top of the Reifling Formation, partly it rests on shallow-water limestones. After TOLLMANN (1976) the Schreyeralmkalk is regarded as a variety of the Hallstatt Limestone. The ammonite and conodont faunas of the Schreyeralm Limestone indicate Pelsonian to Ladinian age.

As both limestone types may be developed on top of the Reifling Formation, Schreyeralmkalk and Schusterbergkalk are frequently used synonymously (TOLLMANN, 1976).

In the Middle Triassic of the Dobratsch Massif (Drau Range) variegated, frequently red pelagic limestones ("Buntkalke"), associated with volcanic rocks, are developed. In the lower block (Liegendscholle) the "Buntkalke" consist of grey, greenish and red nodular limestones. In the lowermost red limestone bed lies the boundary between the *Trinodosus* and *Reitzi* zones. The entire stratigraphic range is Illyrian to Late Langobardian. In the upper block (Hangendscholle) the „Buntkalke" are composed of *Michelinoceras* and ammonite-bearing limestones, bedded limestones and nodular limestones. The sequence is dated as latest Anisian to Langobardian (COLINS & NACHTMANN, 1974; BECHSTÄDT, 1978; BECHSTÄDT et al., 1976). "Buntkalke" and overlying volcanic rocks are only known from the Dobratsch Massif and lacking in all other parts of the Drau Range.

The facies, thickness and age of this sequence is surprisingly similar to the Loibl Formation and superposed volcanics of the Southern Karawanken Mountains.

6. Systematic part

If not stated otherwise, all figured specimens are from the Weiße Wand Member of the Loibl Formation at the type locality Weiße Wand west of the Loibl Pass, Southern Karawanken, Austria. This locality (locality 1 in Fig. 1) is the type locality of most of the described new species. Type stratum are the 60 cm thick red nodular limestones in

the upper part of the Weiße Wand Member. It belongs to the *Tiborella florida* Subzone of the *Spongosilicarmiger transitus* Zone of the upper Illyrian (uppermost Anisian). The section and the position of the samples are shown in Fig. 3. The material from the Weiße Wand Member is housed in the collection of the Institute of Geology and Paleontology of the Innsbruck University.

<div align="center">

Subclass Radiolaria MÜLLER, 1858
Order Polycystida EHRENBERG, 1838
Suborder Entactinaria KOZUR & MOSTLER, 1982
Superfamily Palaeoscenidiacea RIEDEL, 1967
emend. KOZUR & MOSTLER, 1982
Family Eptingiidae DUMITRICĂ, 1978a

</div>

Genus *Eptingium* DUMITRICĂ, 1978a

Type species: *Eptingium manfredi* DUMITRICĂ, 1978a

<div align="center">

Eptingium manfredi manfredi
DUMITRICĂ, 1978a
(Pl. 10, Figs. 1–4, 6, 10)

</div>

1978a *Eptingium manfredi* n. sp., pars – DUMI-TRICĂ, p. 33-34, Pl. 3, Figs. 3, 4; Pl. 4, Figs. 1, 2, 3, 6, 7 (7), non ! Fig. 5

1979 *Eptingium manfredi* DUMITRICĂ – PESSA-GNO, FINCH & ABBOTT, Pl. 6, Figs. 9–11

1980 *Eptingium manfredi manfredi* DUMITRICĂ, 1978 – DUMITRICĂ, KOZUR & MOSTLER, p. 19–20, Pl. 3, Figs. 1–3; Pl. 6, Figs. 5–7

1982 *Eptingium manfredi* DUMITRICĂ – DE WEVER, p. 275–276, Pl. 35, Fig. 5

1982 *Eptingium* cf. *manfredi* DUMITRICĂ – YAO et al., Pl. 1, Fig. 12

1982 *Eptingium* cf. *manfredi manfredi* DUMI-TRICĂ – TAKASHIMA & KOIKE, Pl. 1, Figs. 7, 8

1982 *Tripocyclia* (?) sp. β, pars – MIZUTANI & KOIKE, Pl. 3, Fig. 5

1982 *Tripocyclia* (?) sp. α, pars - MIZUTANI & KOIKE, Pl. 3, Fig. 7

1982 *Eptingium* cf. *manfredi* DUMITRICĂ – MATSUDA & ISOZAKI, Pl. 3, Fig. 25

1982 *Eptingium manfredi* DUMITRICĂ – SATO, NIZHIZONO & MURATA, Pl. 2, Fig. 13

1982 *Eptingium* cf. *manfredi* DUMITRICĂ – YAO, p. 55, Pl. 1, Fig. 17

1988 *Eptingium manfredi* DUMITRICĂ – BRAGIN, OLEJNIK & PARNJAKOV, Pl. 2, Fig. 5

1990 *Eptingium manfredi* DUMITRICĂ – YEH, p. 23, Pl. 6, Figs. 4, 5, 8, 9

1990 *Eptingium manfredi* DUMITRICĂ, 1978a – GORIČAN & BUSER, p. 144, Pl. 8, Figs. 7, 8

1991 *Eptingium manfredi* DUMITRICĂ, 1978 – BRAGIN, p. 109, Pl. 2, Figs. 12, 13

1991 *Eptingium manfredi* DUMITRICĂ, 1978 – KOLAR-JURKOVŠEK, p. 82–83, Pl. 10, Figs. 4 a, 4 b

1993 *Eptingium manfredi* DUMITRICĂ, 1978 – DOSZTÁLY, Pl. 1, Fig. 7

1993 *Eptingium manfredi* DUMITRICĂ, 1978 – FENG, QINGLAI & LIU BENPEI, p. 544–545, Pl. 1, Figs. 14, 15

1994 *Eptingium manfredi manfredi* DUMITRICĂ, 1978 – KOZUR & MOSTLER, p. 42, Pl. 1, Fig. 3

1994 *Eptingium* cf. *manfredi* DUMITRICĂ - NA-KAZAWA, ISHIBASHI, KIMURA, KOIKE, SHI-MIZU & YAO, Pl. 2, Fig. 6

Occurrence: *Spongosilicarmiger transitus* Zone (upper Illyrian) and Fassanian. Very common in Japan, Philippines and in the Tethys.

Remarks: *Eptingium manfredi manfredi* is characterized by unequal angles between the spines and very broad blades with narrow and deep secondary median furrow that may be as deep and wide as the primary furrows between the blades. The distal ends of the spines are pointed or narrowly rounded.

Eptingium manfredi japonicum (NAKASEKO & NISHIMURA, 1979) displays the same unequal angles between the three spines and the same shape of the spines. However, the slightly twisted spines have undivided, narrow to moderately wide blades.

Eptingium manfredi robustum KOZUR & MOST-LER, 1980 (in DUMITRICĂ et al., 1980) displays spi-

nes with broadly rounded distal end and well separated terminal needle-like spine.

These three subspecies have different stratigraphic ranges. *E. manfredi japonicum* is restricted to the Illyrian, *E. manfredi manfredi* begins in the upper Illyrian *S. transitus* Zone and ranges throughout the Fassanian and *E. manfredi robustum* is restricted to the Fassanian.

The Illyrian *Eptingium nakasekoi* KOZUR & MOSTLER, 1994, has equal angles between the spines and the undivided blades are narrow.

The likewise Illyrian *Eptingium ramovsi* n. sp. has distinctly twisted spines with narrow, undivided blades.

Eptingium manfredi japonicum NAKASEKO & NISHIMURA, 1979
(Pl. 10, Fig. 7)

1979   *Tripocyclia japonica* NAKASEKO and NISHIMURA, n. sp., pars – NAKASEKO & NISHIMURA, p. 73, Pl. 4, Figs. 4, 5, non ! Fig. 6

1993   *Eptingium manfredi* DUMITRICĂ, 1978 – SASHIDA, NISHIMURA, IGO, KAZAMA & KAMATA, p. 82, 84, Figs. 6–1, 2

1993   *Eptingium* ? sp., pars – SASHIDA, NISHIMURA, IGO, KAZAMA & KAMATA, p. 84, only Fig. 6–5

1995   *Eptingium nakasekoi* KOZUR & MOSTLER, 1994 - RAMOVŠ & GORIČAN, p. 185, Pl. 5, Figs. 9 (?), 10

Occurrence: Upper part of *T. laevis* Zone and *S. transitus* Zone (upper Illyrian) of Japan, Austria, Hungary, Italy and Slovenia.

Remarks: RAMOVŠ & GORIČAN (1995) assigned the holotypus of "*Tripocyclia*" *japonica* NAKASEKO & NISHIMURA, 1979, and one of the paratypes to *E. manfredi*, the other paratype with strongly twisted main spines to a different species *Eptingium* sp. A. We agree with this assignment and describe *Eptingium* sp. A as *Eptingium ramovsi* n. sp. The holotype of "*T.*" *japonica* can be maintained as primitive subspecies of *E. manfredi* that is transitional between *E. nakasekoi* and *E. manfredi.*

One angle between the three main spines is in general considerably larger than the other two angles, as in typical *E. manfredi manfredi* and the form of the spines is also identical with those of *E. manfredi manfredi*. However, the nominate subspecies has a deep, in primitive forms narrow, in advanced forms broad secondary median furrow on the very broad blades. The holotype has proximally broad, flat blades on the spines, but without median furrow. The paratype (NAKASEKO & NISHIMURA, 1979, Pl. 4, Fig. 4) has a short, very shallow deepening in the proximal part of the blades, but no real median furrow. Such forms can be regarded as transitional forms to *E. manfredi manfredi*.

RAMOVŠ & GORIČAN (1995) assigned a typical *E. manfredi japonicum* and a transition form to *E. nakasekoi* to the latter species.

Eptingium nakasekoi KOZUR & MOSTLER, 1994
(Pl. 11, Fig. 11)

1979   *Tripocyclia* cf. *acythus* DE WEVER – NAKASEKO & NISHIMURA, p. 72–73, Pl. 4, Figs. 1–3

1982   *Tripocyclia* sp. cf. *T. acythus* DE WEVER – KIDO, Pl. 1, Fig. 7

1989   *Eptingium* (?) sp. A – CHENG, p. 147, Pl. 6, Fig. 9

1993   *Eptingium* ? sp., pars – SASHIDA, NISHIMURA, IGO, KAZAMA & KAMATA, p. 84, Figs. 3, 4

1994   *Eptingium nakasekoi* n. sp. - KOZUR & MOSTLER, p. 43, Pl. 1, Fig. 5

Occurrence: Lower and middle Illyrian, advanced forms rarely in the lower *S. transitus* Zone; Japan, Philippines, Austria.

Remarks: For the first time the spicular system of *E. nakasekoi* was recognized. As in the other *Eptingium* species, it consists of a short median bar and 7 spines that originate from the ends of the median bar. All bars are connected by arches. The three blades of each main spine originate from one spine and two arches of the spicular system

E. nakasekoi is the stratigraphically oldest species of the *E. manfredi* lineage. Typical forms occur

in the lower and middle Illyrian. The angles between the main spines are all equal and the blades of the main spines are very narrow. Advanced forms, in which the blades are slightly broader, but also in the proximal part not yet flat, occur in the lower *S. transitus* Zone of the upper Illyrian. In the upper *T. laevis* Zone the first *E. manfredi japonicum* appear. This subspecies is a transitional form between *E. nakasekoi* and *E. manfredi manfredi* that appeared in the *S. transitus* Zone. In typical *E. manfredi japonicum* one angle between the main spines is considerably larger than the other two angles. The blades are proximally broad and in the flat middle part a very shallow grove may be present. Transitional forms to *E. nakasekoi* have still three equal angles between the main spines, transitional forms to *E. manfredi manfredi* have already a shallow grove in the median part of the blades. In *E. manfredi manfredi* a narrow, but deep median grove is present. In advanced forms and above all in the Lower Ladinian *E. manfredi robustum* these secondary groves become as wide as the primary ones. Moreover, in *E. manfredi robustum* the distal ends of the main spines are broadly rounded and display a clearly separated needle-like terminal spine.

Eptingium ramovsi n. sp.
(Pl. 4, Fig. 13; Pl. 10, Fig. 8)

1979 *Tripocyclia japonica* NAKASEKO˙ and NISHIMURA, n. sp., pars – NAKASEKO & NISHIMURA, p. 73, Pl. 4, Fig. 6, non ! Figs. 4, 5

1994 *Eptingium manfredi japonicum* (NAKASEKO & NISHIMURA, 1979) – KOZUR & MOSTLER,, p. 42-43, Pl. 1, Fig. 4

1995 *Eptingium* sp. A – RAMOVŠ & GORIČAN, p. 185, Pl. 5, Figs. 4, 5

Derivatio nominis: In honour of Prof. Dr. A. RAMOVŠ for his outstanding work on Paleozoic and Triassic microfaunas of Slovenia.

Holotypus: The specimen figured by RAMOVŠ & GORIČAN (1975) on Pl. 5, Fig. 5; rep.-no. 650629.

Locus typicus: Tourist path from Tacen through Spodnja Kuhinja to the top of Šmarna Gora,

about 10 km NNW of the centre of Ljubljana, Slovenia, see RAMOVŠ & GORIČAN (1995, Fig. 1).

Stratum typicum: Red cherty limestone, sample 3R (see RAMOVŠ & GORIČAN (1995, Fig. 2); *S. transitus* Zone (uppermost Illyrian).

Material: 14 specimens.

Diagnosis: *Eptingium* with twisted main spines, in which the three blades are narrow and always undivided. On angle between the main spines is nearly 180°, the other two angles are distinctly smaller.

Description: The shell is subspherical and double-layered. The vertices of the outer pore frames have nodes. The inner layer has very small pores. The three main spines are broad and short. They are mostly somewhat shorter than the shell diameter, only exceptionally somewhat longer. They are three-bladed and distinctly twisted. The blades are narrow, without median grove, and separated by deep and wide furrows. The spicular system is bar-centred. At one end of the bar there are three, on the other end four spines. The three blades of the main spines are each connected with one spine and two arches between the spines.

Measurements:

Diameter of shell: 90–135 µm

Length of main spine: 75–135 µm

Basal diameter of main spines: 45–60 µm

Occurrence: *T. laevis* Zone and *S. transitus* Zone (Illyrian) of Japan, Hungary, Austria, Italy and Slovenia.

Remarks: The figured material by RAMOVŠ & GORIČAN (1995) is better preserved and therefore the holotype was chosen from this material.

Eptingium nakasekoi KOZUR & MOSTLER, 1994, is most similar to the new species, but the main spines are untwisted or only slightly twisted and the size of all three angles between the main spines is the same.

Some specimens of *Eptingium manfredi* DUMITRICĂ, 1978a, have twisted main spines, but in these forms the very broad blades have a deep median furrow.

Genus *Cryptostephanidium*
DUMITRICĂ, 1978a

Type species: *Cryptostephanidium cornigerum* DUMITRICĂ, 1978a

Cryptostephanidium cornigerum
DUMITRICĂ, 1978a
(Pl. 10, Fig. 12)

1978a *Cryptostephanidium cornigerum* n. sp. – DUMITRICĂ, p. 31, Pl. 1, Figs. 1–4; Pl. 4, Fig. 4

1982 *Cryptostephanidium* cf. *cornigerum* DU-MITRICĂ – YAO, Pl. 1, Fig. 16

1990 *Cryptostephanidium cornigerum* DUMI-TRICĂ, 1978a – GORIČAN & BUSER, p. 142, Pl. 8, Figs. 1-3

1990 *Cryptostephanidium cornigerum* DUMI-TRICĂ – YEH, p. 22-23, Pl. 5, Figs. 11, 15; Pl. 11, Fig. 5

1995 *Cryptostephanidium cornigerum* DUMI-TRICĂ, 1979 – RAMOVŠ & GORIČAN, p. 184, Pl. 5, Fig. 3

Occurrence: Upper Anisian and Lower Ladinian; Japan, Philippines. Austria, Hungary, Italy, Romania, Slovenia.

Genus *Spongostephanidium*
DUMITRICĂ, 1978a emend.

Type species: *Spongostephanidium spongiosum* DUMITRICĂ, 1978a

Remarks: *Spongostephanidium* was separated originally from other Eptingiidae DUMITRICĂ, 1978a, by its spongy shell and missing spine D in the entactinarian spicular system. The spongy shell developed by fusion of irregular apophyses and short oblique spines at the vertices of a latticed shell. In the most similar genus *Cryptostephanidium* DUMITRICĂ, 1978a, spine D of the entactinarian spicular system is very short and sometimes missing within the same species. On the other hand, in few specimens of *S. spongiosum*, a very short spine D is present. Consequently, both

features chosen by DUMITRICĂ (1978a) to separate *Spongostephanidium* from ·*Cryptostephanidium* (and other Eptingiidae) cannot be used. However, *Spongostephanidium* is used herein for a very distinctive species group with round, needle-like spines. *Cryptostephanidium* is distinguished by three-bladed spines. This difference could not be estimated by DUMITRICĂ (1978a), because in that time only one species of *Spongostephanidium* and two species of *Cryptostephanidium* were known. *Spongostephanidium* in the new scope occurs from the Olenekian up to the Lower Carnian. It is very common in the Olenekian and Anisian, but very rare in Lower Ladinian and younger beds. *Cryptostephanidium* evolved in lowermost Anisian from *Spongostephanidium* and occurs in the entire Middle and Upper Triassic. The transition form between *Spongostephanidium* and Cryptostephanidium, the Lower Anisian *Cryptostephanidium* n. sp. aff. *C. verrucosum* DUMITRICĂ sensu SUGIYAMA (1992) displays proximally bladed and distally round spines. Blades at the very base of the spines as continuations of the connecting spine and arches of the spicular system are present in all *Spongostephanidium* species, but in the new form figured by SUGIYAMA (1992, Fig. 13–3) these blades occupy the entire Lower third of the main spines.

Spongostephanidium japonicum
(NAKASEKO & NISHIMURA, 1979)
(Pl. 6, Figs. 1–3)

1979 *Trilonche japonica* NAKASEKO and NISHI-MURA, n. sp. – NAKASEKO & NISHIMURA, p. 72, Pl. 4, Figs. 8, 10

1989 *Cryptostephanidium* sp. E – CHENG, p. 148, Pl. 7, Fig. 6

1989 Spumellaria gen. et spec. indet. A – CHENG, p. 147, Pl. 6, Fig. 8; Pl. 7, Figs. 1, 2

1989 *Cryptostephanidium* sp. E – CHENG, p. 148, Pl. 7, Fig. 6

1990 *Cryptostephanidium japonicum* (NAKA-SEKO & NISHIMURA) – YEH, p. 22, Pl. 4, Fig. 10; Pl. 5, Figs. 1, 2, 7; Pl. 10, Fig. 11; Pl. 11, Fig. 18

1995 *Cryptostephanidium japonicum* (NAKA-
SEKO & NISHIMURA, 1979) – RAMOVŠ &
GORIČAN, p. 184, Pl. 5, Fig. 1

Occurrence: Upper Anisian of Japan, Philippines, Austria, Hungary, Italy, Slovenia, Turkey. The Lower Ladinian specimen figured by GORIČAN & BUSER (1990) is a new species distinguished by a subquadratic shell.

Remarks: *S. japonicum* is characterized by a spherical shell with very strong and high nodes on the vertices of the pores frames and round, mainly equidistant main spines of the same size that display a slight widening in their middle part. Some of the nodes may be replaced by short, broad, rounded spinules. The widening of the main spines in their middle part is not always distinct and sometimes the spines are cylindrical in their proximal half without recognizable widening.

The main difference from *S. longispinosa* SASHIDA are the high and broad nodes at the vertices and the aequidistant and aequisized main spines.

Spongostephanidium longispinosum SASHIDA, 1991
(Pl. 6, Figs. 4, 5, 6 [?], 8 [?], 11 [?])

1989 *Cryptostephanidium* (?) sp. F – CHENG, p. 148, Pl. 7, Fig. 13
1991 *Spongostephanidium longispinosum* SASHIDA, n. sp. – SASHIDA, p. 694–695, Figs. 7 - 1–8
1992 *Cryptostephanidium longispinosum* (SASHIDA) – SUGIYAMA, p. 1205–1207, Figs. 13 - 1, 2
1993 *Cryptostephanidium longispinosum* (SASHIDA) – NAGAI & MIZUTANI, p. 8, Pl. 2, Figs. 1 (?), 2, 3
1993 *Cryptostephanidium* spp. – NAGAI & MIZUTANI, Pl. 2, Figs. 6, 7
? 1995 *Cryptostephanidium longispinosum* (SASHIDA) – RAMOVŠ & GORIČAN, p. 5, Fig. 2

Occurrence: Common in the Upper Olenekian and Anisian, Japan, Philippines, Austria, Hungary, Italy, Slovenia.

Remarks: According to the above remarks to the genus, this species is again assigned to *Spongostephanidium* as originally proposed by SASHIDA (1991).

Typical of *S. longispinosum* are a spherical shell with short, often oblique spinules or irregular, sometimes branching apophyses at the vertices of the pore frames and needle-like round spines that are not widened in their middle part. In the upper Anisian material the spinules or short, irregular apophyses at the vertices of the pore frame are shorter than in the Upper Olenekian type material, but also in the upper Olenekian such forms are present (SUGIYAMA, 1992, Fig. 13 - 2) indicating that these differences are intraspecific variability. However, these Upper Anisian forms may also have slight widening of the spines in their middle part. Whether they are an independent taxon can only be decided, if very well preserved material from the Anisian forms will be available. The spine D of the spicular system is partly absent, partly very short.

In the Lower Ladinian *Spongostephanidium spongiosum* DUMITRICĂ, 1978a the oblique spinules or short irregular apophyses at the vertices join to a second layer producing a loose spongy shell.

The middle to upper Anisian *Spongostephanidium japonicum* (NAKASEKO & NISHIMURA, 1979) has elongated nodes or short broad spines at the vertices of the pore frames and the round spines are slightly widened in their middle part.

Spongostephanidium austriacum n. sp.
(Pl. 6, Figs. 7, 9)

1989 *Cryptostephanidium* sp. A – CHENG, p. 148, Pl. 6, Fig. 3
1989 *Cryptostephanidium* (?) sp. C – CHENG, p. 148, Pl. 6, Fig. 11
? 1995 *Cryptostephanidium longispinosum* (SASHIDA) -RAMOVŠ & GORIČAN, p. 184, Pl. 5, Fig. 2

Derivatio nominis: According to the occurrence in Austria.

Holotypus: The specimen on Pl. 6, Fig. 9; rep.-no. KKM 1995/I-4.

Material: 23 specimens.

Diagnosis: *Spongostephanidium* with irregular subtriangular to subrectangular shell in equatorial view, large pores, high pore frames without or indistinct nodes at the vertices and three round, not widened main spines of generally unequal length.

Description: The cortical shell has an irregular subtriangular to subrectangular outline in equatorial view. The pores are large and are of different shape. The pore frames are very high, but at the vertices either no nodes or only very small nodes are present. The three round main spines are become slowly but continuously narrower towards the distal end. One spine is generally somewhat to distinctly longer than the other two. The position of the spines is nearly equidistant to distinctly inaequidistant. The arches of the spicular system are very high, overreach often parts of the shell in equatorial view and form three ridges at the base of the spines.

Measurements:

Diameter of shell: 80–100 μm

Length of main spines: 52–76

Maximum width of main spines (without basal blades): 13–16 μm

Occurrence: *S. transitus* Zone (upper Illyrian) of Austria, Hungary, Slovenia and Philippines.

Remarks: *Spongostephanidium japonicum* (NAKASEKO & NISHIMURA, 1979) displays a spherical shell with high nodes at the vertices of the pore frames. Moreover, the main spines are mostly widened in their middle part.

Spongostephanidium longispinosum SASHIDA, 1991, displays a spherical shell and the pore frames have distinct spines or partly branching apophyses at the vertices of the pore frames.

Genus *Triassistephanidium* DUMITRICĂ, 1978a

Type species: *Triassistephanidium laticorne* DUMITRICĂ, 1978a, nom. corr.

Triassistephanidium anisicum n. sp.
(Pl. 10, Figs. 9, 13, 14, 15 [cf.])

Derivatio nominis: According the occurrence in the Anisian.

Holotypus: The specimen on Pl. 10, Fig. 9; rep.-no. KKM 1995/I-3.

Material: 34 specimens, fragile shell mainly destroyed.

Diagnosis: *Triassistephanidium* with broad, but distally pointed spines that have the same width throughout their proximal part.

Description: The shell is in lateral view subtriangular. The pore frames between the wall-inserted arches are fragile and therefore often broken away. The pores are large and of irregular shape. The three main spines are very broad, throughout their proximal part of the same width and distally pointed; rarely the distal end of one or two main spines is narrowly rounded. The blades are very broad and one is subdivided by a shallow furrow. The furrows between the blades are wide, through-like and deep.

The spicular system has a median bar with three and four spines at its ends. All spines are connected by arches that are inserted in the wall. The blades of the main spines are connected with a spine and with three arches; the subdivided main spine (with shallow median furrow) has two connections. Therefore, the spines may be regarded perhaps as four-bladed.

Measurements:

Diameter of shell: 90–105 μm

Length of main spines: 80–120 μm

Maximum width of main spines: 36–50 μm

Occurrence: *S. transitus* Zone (upper Illyrian) of Austria, Hungary and Italy.

Remarks: The lower Ladinian *Triassistephanidium laticorne* DUMITRICĂ, 1978a displays main spines with rounded or blunt distal ends (in general one main spine displays a broadly rounded, the other two a blunt distal end). Moreover, they are distinctly widened somewhat behind the midlength. In transitional forms one or two main spines have rounded distal ends, but also in these forms the main spines are not widened behind the midlength. They are determined as *Triassistephanidium* cf. *anisicum*.

Eptingiidae DUMITRICĂ, 1978; – n. gen. n. sp.
(Pl. 6, Fig. 10)

Remarks: A new genus of four-spined Eptingiidae is present in our material that is distinguished

from the four-spines *Tetrarhopalus* SUGIYAMA, 1992, by the arrangement of all 4 spines in one plane. Unfortunately, the shell are all so much recrystallized that the inner structure could not be observed. Therefore, this new genus cannot yet be described.

Family Hindeosphaeridae
KOZUR & MOSTLER, 1981

Genus *Hindeosphaera*
KOZUR & MOSTLER, 1979

Type species: *Hindeosphaera foremanae* KOZUR & MOSTLER, 1979

Hindeosphaera spinulosa
(NAKASEKO & NISHIMURA, 1979)
(Pl. 4, Figs. 4, 8)

1979   *Archaeospongoprunum spinulosum* NA-KASEKO and NISHIMURA, n. sp. – NAKASE-KO & NISHIMURA, p. 69, Pl. 2, figs. 3, 4, 6

1982   *Archaeospongoprunum spinulosum* NA-KASEKO & NISHIMURA – TAKASHIMA & KOIKE, Pl. 2, Fig. 4

1982   "*Archaeospongoprunum*" *spinulosum* NA-KASEKO & NISHIMURA – MATSUDA & ISOZA-KI, Pl. 3, Figs. 27, 28

?1982   *Archaeospongoprunum spinulosum* NA-KASEKO and NISHIMURA – MIZUTANI & KOIKE, Pl. 3, Fig. 4

1982   *Stylosphaera* (?) *spinulosa* NAKASEKO & NISHIMURA – KISHIDA & SUGANO, Pl. 1, Figs. 16, 17 (?)

1982 *Archaeospongoprunum spinulosum* NAKA-SEKO & NISHIMURA – SATO, NISHIZONO & MURATA, Pl. 2, Fig. 4

1989   *Pseudostylosphaera* sp. cf. *P. spinulosa* (NAKASEKO and NISHIMURA) – CHENG, p. 143, Pl. 6, Fig. 2, Pl. 7, Figs. 8, 9

1989   *Hindeosphaera foremanae* KOZUR et MOSTLER, 1979, *in* B. LAHN, 1984, Pl. 5, Fig. 11 – MARTINI, DE WEVER, ZANINETTI, DENELIAN & KITO, p. 150, Pl. 1, Fig. 15

1989   *Hindeosphaera* sp. – MARTINI, DE WEVER, ZANINETTI, DENELIAN & KITO, p. 150, Pl. 3, Fig. 17

1989   *Hindeosphaera spinulosa* (NAKASEKO et NISHIMURA, 1979) – MARTINI, DE WEVER, ZANINETTI, DENELIAN & KITO, p. 150, Pl. 3, Fig. 8

1989   gen. sp. indet. – MARTINI, DE WEVER, ZA-NINETTI, DENELIAN & KITO, p. 158, Pl. 3, Fig. 15

1990   *Pseudostylosphaera spinulosa* (NAKASE-KO and NISHIMURA) – YEH, p. 15, Pl. 4, Fig. 14

1990   *Hindeosphaera spinulosa* (NAKASEKO & NISHIMURA, 1979) –– DE WEVER, MARTINI & ZANINETTI, p. 586, Pl. 1, Fig. 1

1991   "*Stylosphaera*" *spinulosa* (NAKASEKO et NISHIMURA) – BRAGIN, p. 91, Pl. 3, Figs. 4, 5, 9

1993   *Pseudostylosphaera spinulosa* (NAKASE-KO and NISHIMURA) – SASHIDA, NISHIMU-RA, IGO, KAZAMA & KAMATA, p. 92, Figs. 7-15, 17, 20 (?)

1995   *Hindeosphaera*? *spinulosa* (NAKASEKO & NISHIMURA, 1979) – RAMOVŠ & GORIČAN, p. 185, Pl. 3, Figs. 6-8

Occurrence: Illyrian (*Paraceratites trinodosus* and *Kellnerites felsoeoersensis* ammonoid zones, *Tetraspinocyrtis laevis* and *Spongosilicarmiger transitus* radiolarian zones) of Japan, Philippines, southeast Siberia, Italy, Slovenia, Hungary, Austria.

Remarks: This important Illyrian guide form has variable spines, but a very broad, three-bladed polar spine is always present that is considerably lager than the other spines. Its length, however, is variable. Opposite to this polar spine, but mostly oblique to its axis, a considerably shorter, but in general also broad spine is present. This is the reason that this species was sometimes assigned to *Pseudostylosphaera* KOZUR & MOSTLER, 1981. However, this spine is often not lager than the short by-spines in the antapical hemisphere as typical for *Hindeosphaera*. The vertices of the pore frames bear short spines of different size, but in general they are distinctly larger in the antapical hemisphere, where they may be as long as the antapical spine.

Hindeosphaera spinulosa is the stratigraphically oldest *Hindeosphaera* near *to* the branching point from *Pseudostylosphaera*. For this reason, some specimens are still similar to those *Pseudostylosphaera* species that have polar spines of different size. However, the size differences of the polar spines in *Pseudostylosphaera* are never so strong as in *H. spinulosa*. Moreover, in some specimens the by-spines are as large as the antapical polar spine that is often distinctly moved out of the antapical position. Such forms are already typical *Hindeosphaera*, similar to the advanced Carnian forms.

High variability is often characteristic for the early species of a genus near to its branching point from its ancestral taxon. Because of this high variability, MARTINI et al. (1989) and DE WEVER et al. (1990) assigned *H. spinulosa* to 4 different taxa, two of them in open nomenclature. A rather typical *H. spinulosa* was assigned to *H. foremanae* KOZUR & MOSTLER, 1979 sensu LAHM (1984, Pl. 5, Fig. 11)). However, the specimen figured by LAHM (1984) is a typical middle Carnian *H. foremanae* with slender, distinctly twisted polar spine, totally different from the Anisian *H. spinulosa*.

Genus *Pseudostylosphaera*
KOZUR & MOSTLER, 1981

Type species: *Pseudostylosphaera gracilis* KOZUR & MOSTLER, 1981

Pseudostylosphaera coccostyla acrior
(BRAGIN, 1986)
(Pl. 6, Figs. 12–14)

1979 *Archaeospongoprunum compactum* NA-KASEKO and NISHIMURA, n. sp., pars – NA-KASEKO & NISHIMURA, p. 68, Pl. 1, Fig. 3, non ! Fig. 7

1982 *Archaeospongoprunum* sp. cf. *A. japonicum* NAKASEKO and NISHIMURA, 1979 – KOJIMA, Pl. 2, Fig. 7

1982 *Archaeospongoprunum compactum* NA-KASEKO and NISHIMURA – MIZUTANI & KOIKE, Pl. 3, Fig. 1

1982 *Stylosphaera* (?) *japonica* (NAKASEKO et NISHIMURA, 1979), pars – KISHIDA & SUGANO, Pl. 2, Fig. 13

1982 *Archaeospongoprunum compactum* NA-KASEKO & NISHIMURA – SATO, NISHIZONO & MURATA, Pl. 2, Fig. 3

1986 *Archaeospongoprunum (?) acrior* sp. nov. – BRAGIN, p. 69, Pl. 2, Fig. 5

1988 *"Archaeospongoprunum" acrior* BRAGIN – BRAGIN, OLEJNIK & PARNJAKOV, p. 25, Pl. 2, Fig. 4

1989 *Pseudostylosphaera coccostyla* RÜST, pars – MARTINI, DE WEVER, ZANINETTI, DENELIAN & KITO, p. 150, Pl. 1, Fig. 17, Pl. 2, Figs. 11, 12, 16, Pl. 3, Figs. 10, 11

1990 *Pseudostylosphaera compacta* (NAKASE-KO and NISHIMURA) – YEH, p. 15, Pl. 4, Figs. 3, 4, 20

1991 *Pseudostylosphaera coccostyla* (RÜST) – DOSZTÁLY, Pl. 4, Fig. 3

1992 *Archaeospongoprunum compactum* NA-KASEKO et NISHIMURA – FENG, QINGLAI, Pl. 2, Fig. 5

1993 *Pseudostylosphaera japonica* (NAKASE-KO and NISHIMURA) - SASHIDA, NISHINURA, IGO, KAZAMA & KAMATA, p. 89, 7-9, 15

1993 *Archaeospongoprunum compactum* NAKA-SEKO et NISHIMURA, 1979 – FENG, QINGLAI & LIU BENPEI, p. 542, Pl. 1, Figs. 1, 2

1993 *Archaeospongoprunum japonicum* NA-KASEKO & NISHIMURA, 1979 – FENG, QINGLAI & LIU BENPEI, p. 542, Pl. 1, Fig. 3

1994 *Pseudostylosphaera coccostyla compacta* (NAKASEKO & NISHIMURA, 1979) – KOZUR & MOSTLER, p. 44, Pl. 1, Fig 8

Occurrence: Illyrian (common) and Lower Ladinian (rare) of Japan, Philippines, SE Siberia, Austria, Hungary and Italy.

Remarks: *Pseudostylosphaera coccostyla coccostyla* (RÜST, 1892) displays a secondary furrow in the ridges of the polar spines.

Pseudostylosphaera compacta (NAKASEKO & NISHIMURA, 1979) emend. has longer polar spines.

Pseudostylosphaera compacta (Nakaseko & Nishimura, 1979) emend.
(Pl. 6, Fig. 17)

1979 *Archaeospongoprunum compactum* Na-
KASEKO andNishimura, n. sp. – Nakase-
ko & Nishimura, p. 68, Pl. 1, Fig. 7, non !
Fig. 3

1982 *Archaeospongoprunum compactum* Na-
KASEKO & Nishimura – Takashima &
Koike, Pl. 2, Fig. 3

Occurrence: Illyrian of Japan, Austria, Hungary
and Italy.

Remarks: Nakaseko & Nishimura (1979) figu-
red under *Archaeospongoprunum compactum*
two different species.

The paratype is a very robust form with
broad polar spines that are about 1.2 x longer
than the axial diameter of the cortical shell.
These forms are closely related to *P. coccostyla*
(Rüst, 1892), but have a more subspherical
shell and the blades of the robust main are roun-
ded and have no secondary furrow. The polar
spines are mostly somewhat longer than the
axial diameter of the shell, but partly of the
same length (length of polar spine: axial dia-
meter of shell = 1:1; 3:1).

The holotype has a subspherical shell and rather
long polar spines (about 1.5 x longer than the axial
diameter of the shell). The polar spines are at least
in the proximal half parallel-sided and only in the
distal half there width decreases. *P. compactum* is
restricted to these forms that are transitional forms
between *P. coccostyla* (Rüst, 1892) and *P. longi-
spinosa* Kozur & Mostler, 1981. *P. coccostyla*
has broader and shorter spines, in typical (Lower
Ladinian) forms with a median furrow on the bla-
des of the polar spines and an ellipsoidal cortical
shell.

The Lower Ladinian *P. longispinosa* displays
longer spines (around twice as long as the axial
diameter of the globular shell) and the spines are
more slender. Transitional forms form the basal
Ladinian displays polar spines as slender as in *P.
longispinosa* that are around 1.7 x longer than the
axial diameter of the shell (,,*Stylosphaera*" com-
pacta sensu Bragin, 1991).

Pseudostylosphaera japonica (Nakaseko & Nishimura, 1979)
(Pl. 6, Fig. 15)

1979 *Archaeospongoprunum japonicum* (Naka-
seko and Nishimura, n. sp. – Nakaseko &
Nishimura, p. 68-69, Pl. 1, figs. 2, 4, 9 (?)

1981 *Pseudostylosphaera japonica* (Nakase-
ko & Nishimura, 1979) – Kozur &
Mostler, 1981, p. 32

1982 *Archaeospongoprunum japonicum* Na-
KASEKO and Nishimura – Mizutani &
Koike, Pl. 3, Fig. 3

1982 *Stylosphaera* (?) *japonica* (Nakaseko et
Nishimura, 1979), pars – Kishida & Su-
gano, Pl. 2, Figs. 10, 12

1982 *Archaeospongoprunum japonicum* Na-
KASEKO & Nishimura – Sato, Nishizono
& Murata, Pl. 2, Figs. 1, 2

1982 *Archaeospongoprunum japonicum* Na-
KASEKO and Nishimura – Yao, p. 55, Pl. 1,
Fig. 21

1988 "*Archaeospongoprunum*" *japonicum* Na-
KASEKO, Nishimura – Bragin, Olejnik &
Parnjakov, Pl. 2, Fig. 3

1989 *Pseudostylosphaera japonica* (Nakase-
ko and Nishimura, 1979)- Cheng, p. 143,
Pl. 6, Fig. 1, Pl. 7, Fig. 7

1990 *Pseudostylosphaera japonica* (Nakase-
ko & Nishimura)- Yeh, p. 15, Pl. 4,
Figs. 5–7

1991 "*Stylosphaera japonica*" (Nakaseko et Nis-
himura), pars – Bragin, p. 91, Pl. 1, Fig. 11

1991 *Pseudostylosphaera coccostyla* (Rüst),
pars – Kolar—Jurkovšek, p. 75, 76,
Pl. 5, Figs. 4 a, 4 b

1994 *Pseudostylosphaera japonicum* Nakaza-
WA, Ishibashi, Kimura, Koike, Shimizu
& Yao, Pl. 2, Fig. 7

Occurrence: Illyrian (Upper Anisian) of Japan,
Philippines, SE Siberia, Hungary, Austria.

Remarks: This species was in general correctly
determined, but sometimes the Lower Ladinian *P.
postjaponica* Kozur & Mostler, 1994, that has
the same shape of the polar spines (broadest in or
somewhat behind the midlength) was determined
as *P. japonica* (e.g. Lahm, 1984). In this species

the polar spines are distinctly longer than the long axis of the cortical shell.

Pseudostylosphaera goricanae n. sp.

1995   Pseudosepsagon ? aff. *illyricus* KOZUR & MOSTLER, 1994, pars – RAMOVŠ & GORIČAN, p. 189, Pl. 2, Figs. 1–5, non ! Figs. 6–9

Derivatio nominis: In honour of Dr. Š. GORIČAN, Ljubljana, for her outstanding radiolarian studies.

Holotypus: the specimen figured by RAMOVŠ & GORIČAN (1995) on Pl. 2, Fig. 2; rep.-no. 951204.

Locus typicus: Tourist path from Tacen through Spodnja Kuhinja to the top of Šmarna Gora, about 10 km NNW of the centre of Ljubljana, Slovenia, see RAMOVŠ & GORIČAN (1995, Fig. 1).

Stratum typicum: Red cherty limestone, sample 3R/3 (see RAMOVŠ & GORIČAN , 1995, Fig. 2); *S. transitus* Zone (uppermost Illyrian).

Diagnosis: *Pseudostylosphaera* with two-layered globular shell and twisted three-bladed polar spines that are about as long as the shell diameter. Blades of the polar spines narrow and furrows between them wide and deep.

Description: The cortical shell is globular, double layered. The outer pore frames encloses moderately large, triangular to pentagonal pores. The inner layer displays small pores. The vertices of the outer pore frames bear nodes. The polar spines have about the same length as the shell diameter, but they may have a long, needle-like round terminal spine. They are widest in the beginning of the distal third. The polar spines have three twisted narrow blades. The furrows between them are broad and deep. Inner structure not known.

Measurements:

Diameter of shell: 93–133 μm

Length of polar spines (without terminal needle-like spine: 93–113 μm

Maximum width of polar spines: 29–47 μm

Occurrence: *S. transitus* Zone (uppermost Illyrian) of Hungary, Austria and Slovenia.

Remarks: In our material only badly preserved fragments of this species are present that are, however determinable because of the twisted polar spines. For this reason a fully preserved specimen of the material figured by RAMOVŠ & GORIČAN (1995) was taken as holotype.

Pseudostylosphaera with twisted spines are typical for the Upper Triassic, especially for the Carnian. They have all deep, but narrow furrows between the at least proximally broad blades. The only other Middle Triassic *Pseudostylosphaera* with distinctly twisted spines is the Longobardian *P. helicata* (NAKASEKO & NISHIMURA, 1979). This species displays also narrow blades and wide deep furrows between them. However, it has an ellipsoidal cortical shell and the spines are distinctly longer than the long axis of the shell.

RAMOVŠ & GORIČAN (1995) assigned *Pseudostylosphaera goricanae* together with six-rayed forms to *Pseudosepsagon* ? aff. *illyricus* KOZUR & MOSTLER, 1994. *P. illyricus* is a three-rayed form with 2 additional needle-like spines that belongs to the Sepsagonidae and not to the Hindeosphaeridae as *Pseudostylosphaera*. Forms with polar spines cannot be assigned to this genus. Specimens with two polar spines, but with additionally 4 spines, in which all spines are arranged in three axis that are perpendicular to each other, are assigned to *Hexatortilisphaera* n. gen. They are transitional forms between this genus and *Pseudostylosphaera*.

Genus *Hexatortilisphaera* n. gen.

Derivatio nominis: According to the 6 twisted spines and the spherical cortical shell.

Type species: *Hexatortilisphaera aequispinosa* n. gen. n.sp.

Diagnosis: The cortical shell is spherical, single or double-layered. The 6 main spines are arranged in 3 perpendicular axis. Two opposite spines may be stronger and form polar spines. The main spines are three-bladed, at least the polar spines and a part of the other main spines are twisted. A medullary shell is present, but its structure is unknown.

Occurrence: *S. transitus* Zone (upper Illyrian) of Austria, Hungary and Slovenia. ? Lower Ladinian of Hungary and Italy.

Assigned species:

Hexatortilisphaera aequispinosa n. gen. n.sp.

? *Hexalonche mesotriassica* KOZUR & MOSTLER, 1981

Hexatortilisphaera bipolaris n. sp.

Remarks: *Hexatortilisphaera bipolaris* n. sp. is a transitional form between the new genus and *Pseudostylosphaera* KOZUR & MOSTLER, 1981. This species displays distinct twisted polar spines as in *Pseudostylosphaera goricanae* n. sp. Additionally, four further spines are present and all spines are arranged in three axis that are perpendicularly to each other as in *Hexatortilisphaera* n. gen. These spines are smaller than the polar spines and only the larger ones among them are twisted. In *Hexatortilisphaera aequispinosa* n. gen. n. sp. all spines have the same size and are twisted.

Hexatortilisphaera aequispinosa n. gen. n.sp.
(Pl. 8, Fig. 7)

Derivatio nominis: According to the main spines of equal length.

Holotypus: The specimen on Pl. 8, Fig. 7; rep.-no KKM 1995/I-21.

Material: 7 specimens.

Diagnosis: The single-layered cortical shell is spherical, has very high pore frames and moderately large subtriangular to pentagonal, partly roundish pores. The six three-bladed twisted main spines of equal length are situated in three axis that are perpendicular to each other.

Description: The single layered cortical shall is spherical. The pore frames are high, but without spines or distinct nodes on the vertices. The pores are somewhat variable in diameter, moderately large, subtriangular to pentagonal, partly roundish. The six main spines are situated in three axis that are arranged perpendicularly to each other. They are moderately broad and rather short, but somewhat longer than the radius of the cortical shell. They are three-bladed and distinctly twisted. The blades are narrow and the furrows between them broad and deep. A needle-like terminal spine may be pre-

sent. The structure of the medullary shell is unknown.

Measurements:

Diameter of the shell: 120–125 μm

Length of polar spines: 66–75 μm

Maximum width of polar spines: 25–30 μm

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian) of Austria.

Remarks: The Lower Ladinian *Hexatortilisphaera* ? *mesotriassica* (KOZUR & MOSTLER, 1981) is larger (diameter of shell ca. 200 μm) and displays relatively shorter (not longer than the shell radius), only slightly twisted main spines. The assignment of this species to *Hexatortilisphaera* is doubtful.

Hexatortilisphaera bipolaris n. sp.

1995 *Pseudosepsagon* ? aff. *illyricus* KOZUR & MOSTLER, 1994, pars – RAMOVŠ & GORIČAN, p. 189, Pl. 2, Figs. 6–9, non ! Figs. 1–5

Derivatio nominis: According to the bipolar arrangement of the two larger main spines.

Holotypus: The specimen figured by RAMOVŠ & GORIČAN (1995) on Pl. 2, Fig. 8; rep.-no. 950727.

Locus typicus: Tourist path from Tacen through Sopdnja Kuhinja to the top of Ämarna Gora, about 10 km NNW of the centre of Ljubljana, Slovenia, see RAMOVŠ & GORIČAN (1995, Fig. 1).

Stratum typicum: Red cherty limestone, sample 3R (see RAMOVŠ & GORIČAN (1995, Fig. 2); *S. transitus* Zone (upper Illyrian).

Diagnosis: The spherical cortical shell is double-layered. Two of the six main spines are larger than the other ones, always twisted and bipolarly arranged. The smaller main spines are situated in two axis perpendicularly to the polar axis and to each other and partly untwisted.

Description: The cortical shell is spherical and thick-walled. It consists of two layers. The pore frames of the outer layer have nodes on the vertices. The pores of the outer layer are moderately large. The inner layer has very small pores. The main spines are situated in three axis that are perpendicular to each other. The polar axis is pronounced by distinctly larger, above all broader polar spines that are always twisted. The other spines are slender and

often also shorter than the polar spines. They are also three-bladed, but only the larger one are twisted. The blades are narrow, the furrows between them are broad and deep. Inner structure unknown.

Measurements:
Diameter of shell: 87–107 µm
Length of Polar spines: 73–127 µm
Maximum width of polar spines: 33-47 µm
Length of second order main spines: 47-80 µm
Maximum width of second order main spines: 13–20 µm

Occurrence: *S. transitus* Zone (upper Illyrian) of Slovenia.

Remarks: Because *Hexatortilisphaera bipolaris* n. sp. is a perfect transitional form between the genera *Pseudostylosphaera* and *Hexatortilisphaera* it is described herein despite of the fact that this species is not present in our material. Such transitional forms are often restricted to a very short interval and therefore difficult to find.

The other *Hexatortilisphaera* species have no more separation in polar spines and main spines of second order. Most similar is *Pseudostylosphaera goricanae* n. sp. that has only polar spines.

Family Parentactiniidae Kozur & Mostler, 1981

Genus *Parentactinia* DUMITRICĂ, 1978b

Type species: *Parentactinia pugnax* DUMITRICĂ, 1978b

Parentactinia pugnax DUMITRICĂ, 1978b
(Pl. 11, Fig. 8)

Occurrence: Upper Anisian and Lower Ladinian, world-wide.

Family Pentactinocarpidae DUMITRICĂ, 1978b

Genus *Pentactinocapsa* DUMITRICĂ, 1978b

Type species: *Pentactinocapsa quadripes* DUMITRICĂ, 1978b

Pentactinocapsa awaensis
(NAKASEKO & NISHIMURA, 1979)
(Text-Fig. 6 a; Pl. 5, Fig. 11; Pl. 9, Fig. 11)

1979   *Acanthosphaera awaensis* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 67, Pl. 1, Figs. 1, 5, 6

1994   *Pentactinocapsa awaensis* (NAKASEKO & NISHIMURA, 1979) – KOZUR & MOSTLER, p. 46, Pl. 2, Figs. 10, 11

1995   *Pentactinocapsa awaensis* (NAKASEKO & NISHIMURA, 1979) – RAMOVŠ & GORIČAN, p. 188, Pl. 4, Fig. 9

Occurrence: Illyrian of Japan, Hungary, Slovenia and Austria.

Remarks: The continuation of the basal spines beyond the shell has a very variable angle against the shell axis.

There are only 4 round spines at the base of the pyramidal part of the shell that originate from short spinules of verticiles of the 4 basal spines. In the other *Pentactinocapsa* species at least 6–8 spines are present in that position.

Pentactinocapsa multispinosa n. sp.
(Text-Figs. 5, 6 b; Pl. 5, Figs. 1–10, 12;
Pl. 9, Figs. 1, 2)

Derivatio nominis: According the high number of spines.

Holotypus: The specimen on Text-Fig. 6 b; rep.-no. 15-8-95/I-17.

Material: More than 100 specimens.

Diagnosis: *Pentactinocapsa* with 11–13 round spines, an apical spine, 4 basal spines and 6–8, mostly 7 spines at the end of two spinules from verticiles that branch off from the basal spines in the lower part of the apical half of the shell. Loose cortical shell with large pores.

Description: The loose cortical shell is in the apical part low pyramidal to subconical; between the lateral and basal spines it has the shape of an inverted cone frustum with very slowly diminishing diameter and below the basal spines the shell is hemilenticular to nearly flat. The pores have different size, but some very large pores are
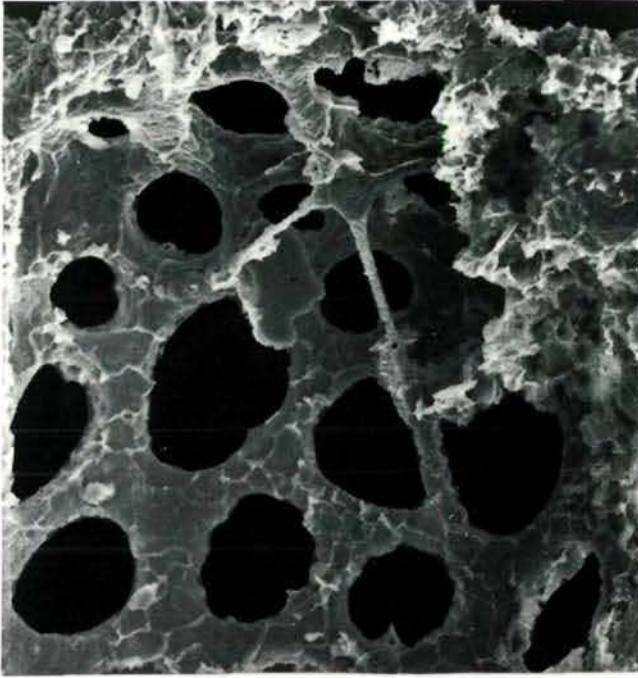
Fig. 5: *Pentctinocapsa multispinosa* n. sp., verticile of the basal spines. Immediately below the verticile, the basal spine is a short distance free. Also the branching lateral spines of the verticile are free adjacent to the verticile. x 500, sample WW 3, rep. no. 15-8-95/1-27.

always present. The pore outline is variable, but always rounded (roundish, oval, rounded rectangular to rounded polygonal, rarely some rounded triangular pores are present). The pentactine spicular system is to its largest part inserted in the shell wall. The round, basally indistinctly rounded four-bladed apical spine is moderately large and free. The 4 basal spines are only distally free and form there outside the shell spines of the same size as the apical spine that are under different angle obliquely outward directed. In the middle part of the apical half of the shell a verticile with two needle-like spinules branch off every basal spine. Below the branching point the basal spine is a short distance free, then again inserted in the shell as above the branching point. The spinules are near the branching point also free, then inserted in the shell (see Text-Fig. 5). At their end a spine of the same length and shape as the apical spine and the basal spines ma be present. Consequently, maximally 8 such spines are present, but because some adjacent spinules may join, the number of the lateral spines varies from 6-8.
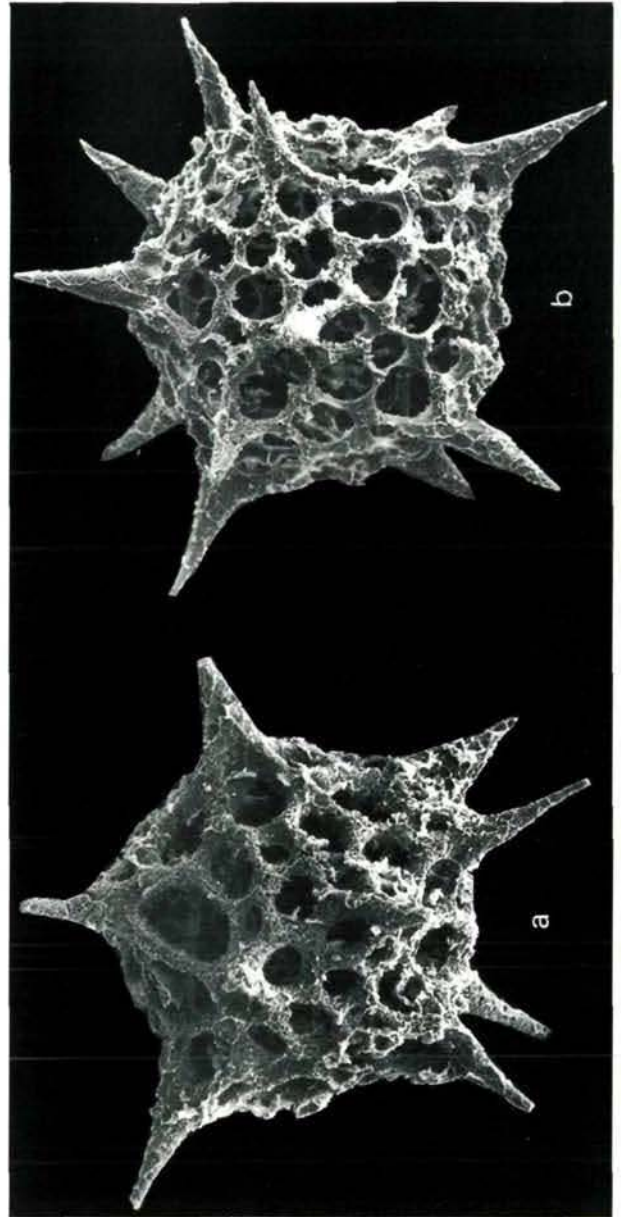

Fig. 6: Comparision of the lateral views of *Pentactinocapsa awaensis* (NAKASEKO & NISHIMURA, 1979) and *P. multispinosa* n. sp. a) *P. awaensis*, x 200, sample WW 12, rep.-no. 15-8-95/1-18. b) *P. multispinosa*, holotype, x 200, sample WW 7, rep.-no. 15-8-95/1-17.

These lateral spines are nearly perpendicular to the shell axis and only a little upward directed.

Measurements:

Axial diameter of heshell: 175–195 μm

Maximum shell diameter perpendicular to the shell axis: 175–235μm

Length of the spines: 60–82 μm

Occurrence: *Spongosilicarmiger transitus* Zone (uppermost Anisian) of Austria and Hungary.

Remarks: *Pentactinocapsa awaensis* (NAKASE-KO & NISHIMURA, 1979) displays maximally 4 lateral spines that are obliquely upward directed.

Genus *Pentactinorbis* DUMITRICĂ, 1978b

Type species: *Pentactinorbis kozuri* DUMITRICĂ, 1978b

Pentactinorbis dumitricai
KOZUR & MOSTLER, 1994
(Pl. 9, Figs. 3, 4 (?), 5, 6, 7–9 (?), 10, 14)

1994   *Pentactinorbis dumitricai* n. sp. – KOZUR & MOSTLER, p. 47-48, Pl. 3, Figs. 4-7
1995   *Pentactinorbis dumitricai* KOZUR & MOSTLER, 1994 – RAMOVŠ & GORIČAN, p. 188, Pl. 4, Figs. 10, 12

Occurrence: Illyrian of Austria, Hungary and Slovenia.

Remarks: The small spinules on the pentactine spicular system cannot be recognized in our material. However, this is surely preservation controlled, because the type material is of excellent preservation, the herein described material is only of moderate preservation. In the material figured by RAMOVŠ & GORIČAN (1995) these spinules are also not recognizable.In some specimens, the spines are distinctly longer (Pl. 9, Figs. 7–9); they are determined as *Pentactinorbis* cf. *dumitricai*. A similar form is figured by RAMOVŠ & GORIČAN (1995, Pl. 4, Fig. 12). This may be intraspecific variability. However, such forms are so far only known from the *S. transitus* Zone of the upper Illyrian and not form the immediately underlying *Tetraspinocyrtis laevis* Zone.

Family Sepasagonidae Kozur & Mostler, 1981

Genus *Parasepsagon*
DUMITRICĂ, KOZUR & MOSTLER, 1980

Type species: *Parasepsagon tetracanthus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Parasepsagon variabilis
(NAKASEKO & NISHIMURA, 1979)
(Pl. 4, Figs. 2, 3, 7, 9)

1979   *Staurodoras variabilis* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 71-72, Pl. 3, Figs. 5, 8
1989   *Parasepsagon variabilis* (NAKASEKO & NISHIMURA) – YEH, p. 63, Pl. 1, Figs. 16, 19
1991   *Staurolonche* ? *variabilis* (NAKASEKO & NISHIMURA) – BRAGIN, p. 86, Pl. 1, Fig. 16
1995   *Parasepsagon variabilis* (NAKASEKO & NISHIMURA, 1979) – RAMOVŠ & GORIČAN, p. 187, Pl. 3, Fig. 5

Occurrence: Upper Anisian of Japan, SE Siberia, Slovenia, Austria and western North America.

Remarks: Width and length of the spines is variable, but in general one spine is somewhat longer and broader than the other three ones. Characteristically, the three-bladed, untwisted spines are rather short (as long as the outer shell diameter or shorter) and broad. The outer pore frame has nodes at the vertices and enclose larger pores. The inner layer of the cortical shell displays small pores.

In all other known *Parasepsagon* species, the spines are distinctly longer than the shell diameter.

Genus *Pseudosepsagon*
KOZUR & MOSTLER, 1994

Type species: *Pseudosepsagon pentaspinosus* KOZUR & MOSTLER, 1994

RAMOVŠ & GORIČAN (1995) assigned species with 3 twisted main spines and those with additional one or two needle-like spines to *Pseudosepsagon.* Consequently, they included also *Sarla* ? *anisica* into *Pseudosapsagon.* However, *Pseudopsepsagon* is from the transitional field of four-rayed Sepsagonidae to three-rayed ones. In the Illyrian *P. trinodosus* ammonoid zone forms with additional spines (*P. pentaspinosus* KOZUR & MOSTLER, 1994 and *P. illyricus* KOZUR & MOSTLER, 1994) clearly dominate over three-rayed forms without additional spines. In the next younger uppermost Illyrian *Kellnerites fels-*

oeoersensis ammonoid zone forms with additional needle-like spines are already subordinate against forms with three twisted main spines and without additional spines. In Ladinian and younger deposits only forms with three twisted spines are present and forms with additional needle-like spines are missing. Rich Pelsonian faunas are not known. If in these and (or) older deposits only forms with three twisted main spines and additionally one or two needle-like spines are present, then *Pseudosepsagon* should be restricted to these forms. However, if also in this level forms with three twisted spines and with additional needle-like spines occur together, then they should be united in one genus. For the moment, *Sarla* ? *anisica* KOZUR & MOSTLER, 1994 is tentatively assigned to *Pseudosepsagon*.

Pseudosepsagon ? aff. *illyricus* KOZUR & MOSTLER, 1994 sensu RAMOVŠ & GORIČAN (1995) does neither belong to *P. illyricus* KOZUR & MOSTLER, 1994 nor to the genus *Pseudosepsagon*. *P. illyricus* is a three-rayed form with an additional needle-like spine. *Pseudosepsagon* ? *aff illyricus* RAMOVŠ & GORIČAN (1995) comprises typical *Pseudostylosphaera* KOZUR & MOSTLER with two twisted polar spines as well as similar forms with two polar spines that have additionally 4 cross-like arranged spines in the equatorial plane or irregularly arranged spines near the equatorial plane that probably do not belong to the same species (and perhaps even not to *Pseudostylosphaera*).

Pseudosepsagon ? *anisicus*
(KOZUR & MOSTLER, 1994)
(Pl. 4, Figs. 6?, 10)

1994   *Sarla* ? *anisica* n. sp. – KOZUR & MOSTLER, p. 77-78, Pl. 17, Figs. 7, 8

1995   *Pseudosepsagon pentaspinosus* KOZUR·& MOSTLER, 1994, pars – RAMOVŠ & GORIČAN, p. 189, Pl. 3, Figs. 9, 10, 11 (?)

Occurrence: Rare in the middle Illyrian, common in the upper Illyrian (Upper Anisian) of Hungary, Slovenia and Austria.

Remarks: *Pseudosepsagon* ? *anisicus* displays a latticed cortical shell as *Pseudosepsagon pentaspi-*

nosus, but the three main spines are considerably broader and additional needle-like spines are missing. Moreover, the vertices of the pore frames bear exclusively nodes, whereas the vertices of the pore frames in *P. pentaspinosus* bear spines and only some nodes. This latter sculpture of the vertices of the pore frames is present also in *Tripocyclia* sp. B NAKASEKO & NISHIMURA, 1979, *Sarla* sp. A CHENG, 1989, *Sarla* (?) sp. B YEH (1990) that were all assigned to *P. pentaspinosus* by RAMOVŠ & GORIČAN (1995). If these forms without additional needle-like spines belong to *Pseudosepsagon*, then they really do belong to *P. pentaspinosus* as assumed by RAMOVŠ & GORIČAN (1995). However, forms with stout twisted main spines and without additional needle-like spines that display exclusively nodes on the vertices of the pore frames belong to *P.* ? *anisica* as most of the figured material in RAMOVŠ & GORIČAN (1995). In *Pseudosepsagon* ? cf. *anisicus* (Pl. 4, Fig. 6, only one specimen is present) two of the three twisted stout main spines are situated near to each other. May be that this form displays an additional spine, but in its possible position the shell is encrusted with silica.

Family Thalassothamnidae Haecker, 1906

Genus *Triassothamnus*
KOZUR & MOSTLER, 1981

Type species: *Palacantholithus* ? *verticillatus* DUMITRICĂ, 1978b
Synonym: *Archaeothamnulus* DUMITRICĂ, 1982a

Triassothamnus verticillatus
(DUMITRICĂ, 1978b)
(Pl. 11, Fig. 3)

1978b   *Palacantholithus* ? *verticillatus* n.sp. – DUMITRICĂ, p. 42, Pl. 1, Fig. 1; Pl. 2, Fig. 5

1981   *Triassothamnus verticillatus* (DUMITRICĂ, 1978) – KOZUR & MOSTLER, p. 5

1982a   *Archaeothamnulus verticillatus* (DUMITRICĂ) – DUMITRICĂ, p. 418, Pl. 5, Fig,. 3, 4; Pl. 7, Fig. 4

1990 *Triassothamnus verticillatus* (DUMITRICĂ), 1978 b – GORIČAN & BUSER, p. 160, Pl. 7, Fig. 3

Occurrence: *S. transitus* Zone (upper Illyrian) to Lower Ladinian.

Superfamily Hexastylacea HAECKEL, 1882
emend. PETRUSHEVSKAYA, 1979
Family Palhindeolithidae
KOZUR & MOSTLER, 1981

Genus *Tandarnia* DUMITRICĂ, 1982a

Type species: *Tandarnia recoaroense* DUMITRICĂ, 1982a

***Tandarnia recoaroense* DUMITRICĂ, 1982a**
(Pl. 11, Figs. 1, 2, 4-7)

1982a *Tandarnia recoaroense* n. sp. – DUMITRICĂ, p. 415, Pl. 3, Figs. 6–10
1990 *Tandarnia recoaroense* DUMITRICĂ, 1982 – GORIČAN & BUSER, p. 159, Pl. 7, Fig. 4
1995 *Tandarnia recoaroense* DUMITRICĂ, 1982 – RAMOVŠ & GORIČAN, p. 191, Pl. 4, Fig. 11

Occurrence: *S. transitus* Zone (upper Illyrian) and Fassanian of Austria, Hungary and Italy.

Family Tiborellidae Kozur & Mostler, 1994

Genus *Tiborella* DUMITRICĂ, KOZUR & MOSTLER, 1980 (in: DUMITRICĂ et al., 1980)

Type species: *Tiborella magnidentata* DUMITRICĂ, KOZUR & MOSTLER, 1980

Tiborella florida florida
(NAKASEKO & NISHIMURA, 1979)
(Pl. 3, Figs. 5, 13–16)

1979 *Cecrops floridus* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 69–70, Pl. 2, Figs. 5, 8

1991 *Staurolonche floridus* (NAKASEKO et NISHIMURA) – BRAGIN, p. 87, Pl. 10, Fig. 4
1994 *Tiborella florida* (NAKASEKO & NISHIMURA, 1979) – KOZUR & MOSTLER, p. 52
1995 *Tiborella florida* (NAKASEKO & NISHIMURA, 1979), pars – RAMOVŠ & GORIČAN, p. 191–192, Pl. 4, Figs. 1-4, non ! Fig. 5

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (uppermost Anisian *Kellnerites felsoeoersensis* ammonoid zone) of Japan, southeastern Siberia, Slovenia and Austria.

Remarks: The knob-like end of the 4 spines is very characteristic for the nominate subspecies. The spines are untwisted or very slightly twisted. Forms with strongly twisted spines and pointed ends that were assigned to *T. florida* by RAMOVŠ & GORIČAN (1995, Pl. 4, Fig. 5) do not belong to this species, but represent a new species that is similar to *T. magnidentata* DUMITRICĂ, KOZUR & MOSTLER, 1980, but distinguished by its rectangular shell outline.

Tiborella sp. A CHENG, 1989 and *Tiborella* sp. A YEH, 1990, both assigned to *Tiborella florida* by RAMOVŠ & GORIČAN (1995) do not belong to the nominate subspecies (*Tiborella* sp. A CHENG, 1989) and not even to *T. florida* respectively (*Tiborella* sp. A YEH, 1990). *Tiborella* sp. A CHENG, 1989 with untwisted, terminally pointed to rounded spines (but without knob-like distal end) belong to *Tiborella florida austriaca* n. subsp., whereas *Tiborella* sp. A YEH, 1990 b with one twisted and 3 untwisted, terminally pointed spines is a *T. anisica* KOZUR & MOSTLER, 1994.

***Tiborella florida austriaca* n. subsp.**
(Pl. 4, figs. 1, 5)

1989 *Tiborella* sp. A – CHENG, p. 147, Pl. 7, Fig. 18

Derivatio nominis: According to the occurrence in Austria.

Holotypus: The specimen on Pl. 4, Fig. 1; rep.-no. KKM 1995/I-1.

Material: 7 specimens.

Diagnosis: *Tiborella* with untwisted spines that are terminally pointed or round, but without knoblike distal thickening.

Description: Outer shell subrectangular to subglobular. The pore frames are highly elevated. The pores are large. The 4 spines are three-bladed, very broad, moderately long. Their length differs slightly within one specimen; one spine may be broader than the others. The distal ends of the spines are rounded (especially in the broader spine) or pointed, but without knob-like thickening. Two ridges of the spines are connected with the ridges of adjacent spines to form a subrectangular frame that is partly overgrown by the pore frames of the shell. The 4 spines continue inside the cortical shell and join a rather small medullary shell with large pores. Internal structure inside the medullary shell not observable in the present material.

Measurements:
Diameter of shell: 130–145 µm
Length of spines: 65–110 µm
Maximum width of spines: 50–65 µm

Occurrence: *T. laevis* Zone and *T. florida* Subzone of the *S. transitus* Zone (Illyrian) of Austria and the Philippines.

Remarks: *Tiborella florida florida* (NAKASEKO & NISHIMURA, 1979) displays somewhat more slender spines with a knob-like distal thickening. The most specimens display a slight torsion of the spines.

Tiborella agria SUGIYAMA, 1992 from the Upper Olenekian of Japan has also untwisted spines, but they are slender and strongly pointed.

In *Tiborella anisica* KOZUR & MOSTLER, 1994, from the Illyrian *Paraceratites trinodosus* ammonoid zone, one spine is strongly twisted and distinctly longer than the other three, untwisted spines.

Family Triposphaeridae VINASSA DE REGNY, 1898 emend. KOZUR & MOSTLER, 1981

Synonym: Entactiniidae RIEDEL, 1967

Genus *Helioentactinia* NAZAROV, 1975

Type species: *Entactinosphaera polyacantha* FOREMAN, 1963
Synonym: *Parentactinosphaera* KOZUR & MOSTLER, 1979

Helioentactinia oertlii (KOZUR & MOSTLER, 1979) (Pl. 7, Fig. 9)

1979   *Parentactinosphaera oertlii* n. sp. – KOZUR & MOSTLER, p. 73–74, Pl. 2, Fig. 2
1981   *Helioentactinia oertlii* (KOZUR & MOSTLER, 1979) – KOZUR & MOSTLER, p. 17, Pl. 2, Figs. 2, 4, 6; Pl. 4, Figs. 1, 2, 7
1984   *Helioentactinia oertlii* (KOZUR & MOSTLER, 1979) – LAHM, p. 19, Pl. 2, Figs. 2, 3

Occurrence: Upper Anisian to Ladinian, ? Carnian of Austria, Hungary and Italy.

Genus *Weverisphaera* KOZUR & MOSTLER, 1981

Type species: *Weverisphaera fassaensis* KOZUR & MOSTLER, 1981
Synonym: *Pseudoheptacladus* LAHM, 1984

Weverisphaera anisica n. sp. (Pl. 8, Fig. 6)

Derivatio nominis: According to the occurrence in the Anisian.

Holotypus: The specimen on Pl. 8, Fig. 6; rep.-no. KKM 1995/I-8.

Material: 15 specimens.

Diagnosis: Cortical shell spherical, small, double-walled. The 7 long, slender, three-bladed main spines are in their proximal half parallel-sided, in the distal part tapering to their pointed distal end.

Description: The spherical, small shell is double-walled. The outer pore frames have moderately large pores, the inner pore frames have small pores. The vertices of the outer pore frames are only a little elevated. The seven equisized main spines are slender, in their proximal half parallel-sided, in their distal half tapering to the pointed distal end. The three blades are rather broad, the furrows between them are narrow and deep. The rounded, needle-like terminal part of the main spines without blades and furrows is very short. Medul-

lary shell present. The structure inside the medullary shell is unknown.

Measurements:

Diameter of cortical shell: 125–135 μm

Length of the main spines: 160–175 μm

Maximum width of the main spines: 25–30 μm

Occurrence: Illyrian of Austria and Hungary.

Remarks: The Lower Ladinian *Weverisphaera fassanica* KOZUR & MOSTLER, 1981, is larger and the distal needle-like round part of the main spines is 1/3 of the entire length of the main spines or longer.

Suborder Spumellaria EHRENBERg, 1875
Superfamily Actinommacea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1979
Family Actinommidae HAECKEL, 1862 emend.
KOZUR & MOSTLER, 1979

Genus *Acanthosphaera* EHRENBERG, 1858

Type species: *Acanthosphaera haliphormis* EHRENBERG, 1861

Acanthosphaera carterae n. sp.
(Pl. 9, Figs. 15–18)

Derivatio nominis: In honour of Dr. Elizabeth S. CARTER, Veronia, for her outstanding contribution to the Upper Triassic an Jurassic radiolarian research.

Holotypus: The specimen on Pl. 9, Fig. 16; rep.-no. KKM 1995/I-12.

Material: 23 specimens.

Diagnosis: Single latticed shell with large, mostly hexagonal and pentagonal pores of different size. 7–10 small, three-bladed spines are present.

Description: The spherical, single latticed shell bears large pores of different size and shape; most of them are hexagonal and pentagonal, but few tetragonal or roundish pores may be also present. The vertices of the pore frames bear tiny spines. Sometimes the pore frames are verrucose. 7–10 small spines of different size are present. At their base they are rather broad and have

there three high blades separated by deep and wide furrows. The distal part of the largest spines among them is needle-like. Two spines, often in subpolar position, are often somewhat larger than the other ones. At least the largest spines continue at the inner side as fragile, needle-like spines.

Measurements:

Diameter of shell: 160–180 μm

Length of the spines: 12–40 μm

Width at the base of the spines: 14–20 μm

Occurrence: Illyrian of Austria, Hungary and Italy.

Acanthosphaera nicorae n. sp.
(Pl. 8, Fig. 9)

Derivatio nominis: In honour of Prof. Dr. Alda NICORA, Milano, for her outstanding contributions to the Triassic micropaleontology and stratigraphy.

Holotypus: The specimen on Pl. 8, Fig. 9; rep.-no. KKM 1995/I-9.

Material: 7 specimens.

Diagnosis: Single spherical shell with large pentagonal and hexagonal pores and 7–8 tricarinate short main spines of equal size.

Description: The single spherical shell displays large pentagonal to hexagonal pores of somewhat variable size. The 7–8 tricarinate main spines are always distinctly shorter than the shell diameter. Their three narrow blades are separated by wide and deep furrows and reach until the distal end. The base of the main spines is rather broad, their width decreases continuously.

Measurements:

Diameter of shell: 113–130 μm

Length of main spines: 65–74 μm

Maximum width of main spines: 17–22 μm

Occurrence: Illyrian of Austria and Hungary.

Remarks: The Middle Carnian *Acanthosphaera mocki* KOZUR & MOSTLER, 1979, has more and shorter spines. It may be the successor of *A. nicorae*. All other known Triassic *Acanthosphaera* species have needle-like, to their largest part round main spines.

Genus Hexalonche HAECKEL, 1882

Type species: *Hexalonche phaenaxonia* HAECKEL, 1887

Hexalonche simplex LAHM, 1984
(Pl. 8, Figs. 1, 4)

1984 *Hexalonche simplex* n. sp. – LAHM, p. 79, Pl. 14, Figs. 2, 3

Occurrence: Upper Anisian – Lower Ladinian.

Hexalonche bragini n. sp.
(Pl. 8, Fig. 5)

Derivatio nominis: In honour of N. Ju. BRAGIN for his important contributions to the knowledge of the Mesozoic radiolarians.

Holotypus: The specimen on Pl. 8, Fig. 5; rep.-no. KKM 1995/I-11.

Material: 3 specimens.

Diagnosis: Small shell with moderately large triangular or tetragonal pores and six very large main spines that become continuously narrower from their broad base towards the pointed distal end.

Description: The shell is small, subspherical, a little elevated below the spines. The pores are moderately large, trigonal or tetragonal, the pore frames are narrow and low. The six spines are relatively to the shell very large. They are situated in three axes that are perpendicular to each other. Their base is broad and they become continuously narrower towards the pointed distal end. The spines are tricarinate with wide and deep furrows. Near their distal end they become needle-like with round cross section. Inner structure unknown.

Measurements:

Diameter of shell: 93–107 μm

Length of the main spines: 179–235 μm

Width of the main spines at their base: 35–42 μm

Occurrence: So far only known from the *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian) at the locality Weiße Wand.

Genus *Triassospongosphaera* KOZUR & MOSTLER, 1981

Type species: *Spongechinus triassicus* KOZUR & MOSTLER, 1979

Triassospongosphaera multispinosa (KOZUR & MOSTLER, 1979)
(Pl. 8, Figs. 8, 12)

1979 *Acanthosphaera* ? *multispinosa* n. sp. KOZUR & MOSTLER, p. 50, Pl. 20, Fig. 3

1981 *Triassospongosphaera multispinosa* (KOZUR & MOSTLER, 1979) – KOZUR & MOSTLER, p. 67, Pl. 58, Fig. 3

1984 *Triassospongosphaera multispinosa* (KOZUR & MOSTLER, 1979) – LAHM, p. 66–67, Pl. 11, Fig. 10

Occurrence: Upper Anisian – Middle Carnian.

Family Ethmopshaeridae HAECKEL, 1862

Genus *Cenosphaera* EHRENBERG, 1854

Type species: *Cenosphaera plutonis* EHRENBERG, 1854

Cenosphaera parvispinosa n. sp.
(Pl. 9, figs. 12, 13)

Derivatio nominis: According to the tiny, needle-like spines at the vertices of the pore frames.

Holotypus: The specimen on Pl. 9, Fig. 13; rep.-no. KKM 1995/I-2.

Material: 31 specimens.

Diagnosis: Latticed shell with tiny spines at the vertices of the pore frames. Pores large, hexagonal and pentagonal.

Description: The spherical shell has large, hexagonal (dominant) and pentagonal pores. The pore frames are high and bear tiny, needle-like spines at the vertices. Few of these spines may be somewhat longer, but they are also very small and needle-like. There are no inner continuations of the spines.

Measurements:

Diameter of the shell: 210–239 μm

Length of the spines at the vertices: In general up to 5 μm, single spines up to 17 μm

Width of the spines at the vertices: In general up to 2 μm, rarely up to 5 μm

Occurrence: Upper Anisian and Lower Ladinian of Austria, Hungary and Italy.

Remarks: The presence of tiny spines in *Cenosphaera* is exceptional, but they are only sculptures on the vertices of the pore frames and have no inner continuations.

Superfamily Centrocubacea
HOLLANDE & ENJUMET, 1960

Family Heptacladidae
DUMITRICĂ, KOZUR & MOSTLER, 1980

Remarks: The polygonal to cubic microsphere of *Heptacladus* consists of 2 opposite pentagonal frames and 5 quadratic frames between them. It is therefore near related to the Centrocubidae as already stated by DUMITRICĂ (1983). Centrocubidae HOLLANDE & ENJUMET, 1960 and Heptacladidae DUMITRICĂ, KOZUR & MOSTLER, 1980 are united in the superfamily Centrocubacea. It is not clear, whether this microsphere is a modified entactinarian spicular system, like in *Lithocubus* HAECKEL, 1882 for the Nassellaria or a special spumellarian medullary shell. For the moment, they are assigned to the Spumellaria. However, a separate superfamily is necessary. The Centrocubidae are restricted to the Neogene Centrocubacea, in which branching verticile spines form a spongy meshwork. In the Heptacladidae, the verticile spines are unbranched and join directly the adjacent spines that originate from the corners of the microsphere. Several other, mostly undescribed families may belong to this superfamily.

Genus *Heptacladus* DUMITRICĂ,
KOZUR & MOSTLER, 1980

Type species: *Heptacladus crassispinus* DUMITRICĂ, KOZUR & MOSTLER, 1980

Heptacladus crassispinus DUMITRICĂ,
KOZUR & MOSTLER, 1980
(Pl. 7, Fig. 12)

Occurrence: Upper Anisian to Lower Ladinian from Austria, Hungary and Italy.

Heptacladus ? *anisicus* n. sp.
(Text-Fig. 7; Pl. 7, Figs. 10, 11, 13, 14)

Derivatio nominis: According to the occurrence in the Anisian.

Holotypus: The specimen on Pl. 7, Fig. 10; rep.-no. KKM 1995/I-5.

Material: 31 specimens.

Diagnosis: The subspherical shell bears needle-like short spines at the vertices. The 4 round, needle-like main spines are very long and very slender, a round medullary shell is present.

Description: The pores of the very large subspherical shell are very large, but of irregular size and shape. The vertices of the pore frames bear small, needle-like spines that may branch at their distal end. The four main spines are not situated in one plane, but are not situated much outside the equatorial plane. They are very long, very slender, needle like. A spherical medullary shell is present that is connected by 6–8 spines with the cortical shell. Four of these spines continue outside the cortical shell as the main spines. Structure inside the medullary shell unknown.

Measurements:

Diameter of the cortical shell: 133–181 μm

Diameter of the medullary shell: 64–69 μm

Length of the main spines: 245–363 μm

Maximum width of the main spines: 17–29

Length of the by-spines at the vertices: 7–29 μm

Occurrence: *S. transitus* Zone (upper Illyrian) at Weiße Wand.

Remarks: Because the structure inside the medullary shell is not known, the assignment to *Heptacladus* is tentative. *Heptacladus crassispinus* DUMITRICĂ, KOZUR & MOSTLER, 1980 is distinguished by the presence of 7 spines and by the absence of a medullary shell.
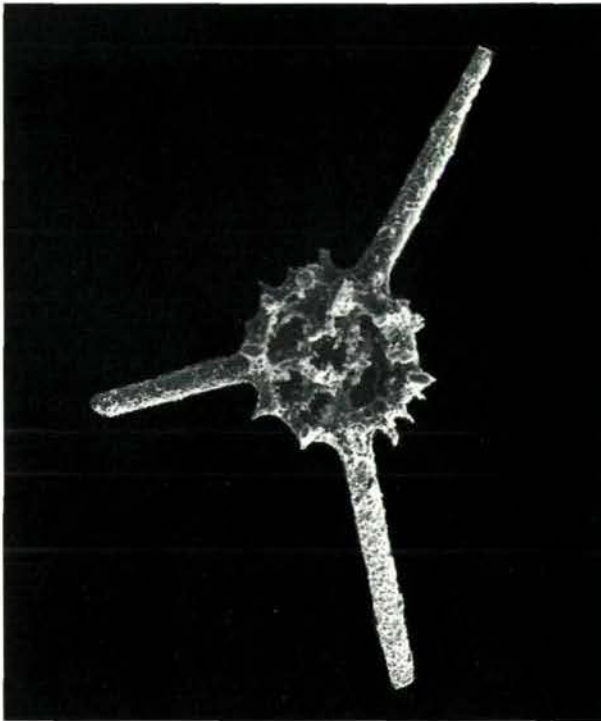
Fig. 7: *Heptacladus anisicus* n. sp., opened specimen with visible medullary shell. x 150. sample WW 4. rep.-no. 15-8-95/I-11.

Genus *Komoella* LAHM, 1984

Type species: *Komoella symmetrica* LAHM, 1984

Komoella symmetrica LAHM, 1984
(Pl. 8, Fig. 2)

1984   *Komoella symmetrica* n. sp. – LAHM, p. 32–33. Pl. 4. Figs. 5, 6

Occurrence: Upper Anisian and Lower Ladinian of Austria, Hungary and Italy.

Remarks: Our material displays beside tiny by-spines at the vertices of the pore frames also few somewhat longer by-spines. Because also in *Heptacladus* the length of the by-spines is very variable, this difference is regarded as intraspecific variability.

Genus *Livinallongella* LAHM, 1984

Type species: *Livinallongella hauseri* LAHM, 1984

Remarks: LAHM (1984) reported the same inner structure as for *Heptacladus* DUMITRICĂ, KOZUR & MOSTLER, 1980, but did not figured this structure. We have opened several specimens of *L. hauseri*, but because of the recrystallisation of our material we could neither confirm nor reject the observations by LAHM (1984). In the assignment of *Livinallongella* to the Heptacladidae we follow LAHM (1984), but this assignment is tentative so long the inner structure cannot be documented.

Livinallongella lahmi n. sp.
(Pl. 7. Figs. 1. 2. 3 [cf.] 4. 5, 6 [cf.]. 7. 8 [aff.])

Derivation of name: In honour of Dr. B. LAHM who recovered the genus *Livinallongella*.

Holotypus: The specimen on Pl. 7. Fig. 2, rep.-no. KKM 1995/I-6.

Material: More than 100 specimens.

Diagnosis: A *Livinallongella*, in which the 7 main spines have after the vertices an oval, rarely triangular cross section, but without furrows. Vertices are present in or after the midlength of the main spines, rarely also before the midlenght.

Description: The cortical shell is spherical to subspherical and often overgrowths a little the base of the 7 main spines. The proximal part of the main spine is three-bladed with three deep furrows. The distal part of the main spines after the vertices is needle-like and has an oval cross section. In transitional forms to *Livinallongella hauseri* LAHM (*Livinallongella* cf. *lahmi*, Pl. 7. Figs. 3, 6) their cross section is triangular, but without furrows. This distal part of the main spines is in general as long as the proximal part, but in some specimens longer. The vertices are situated in or behind the midlength of the main spines, but in some specimens before the midlength. They bear three, needle-like denticles of different length. Often they are as long as or even longer than the distal part of the main spines after the vertices, exceptionally they are very short. The

main spines continue inside the cortical shell and have in the inner part vertices. A medullary shell could not be observed, but the innermost part was always recrystallized.

Measurements:

Diameter of shell: 100–136 μm

Length of the main spines: 133–169 μm

Maximum width of the main spines: 23–31 μm

Length of the distal part of the main spines after the vertices: 35–127 μm

Length of the side-spines at the vertices: 33–154 μm, rarely only 18 μm (*Livinallonga* aff. *lahmi*)

Occurrence: Very common in the *S. transitus* Zone (upper Illyrian) of the Weiße Wand Member of the Weiße Wand section, but surprisingly not yet found outside the type locality.

Remarks: In *Livinallongella hauseri* LAHM, 1984, the distal part of the spines is more than twice as long as the proximal part and it has the same cross section as the proximal part; only its distal end is needle-like with roundish cross section. The spines at the vertices are always considerably shorter (4–5 times) than the distal part of the main spine after the vertices.

Livinallongella lahmi is used in a very broad sense and may include several species. However, the investigated stratigraphic interval (part of a radiolarian subzone is too short to decide whether the observed differences demonstrate very high intraspecific variability or different taxa.

Moreover, rich *Livinallongella* associations occur only in samples WW 12 and WW 13. Thus, possible differences in the range of the rather different morphotypes cannot be estimated.

Genus *Paraheptacladus*
KOZUR & MOSTLER, 1981

Type species: *Paraheptacladus symmetricus* KO-ZUR & MOSTLER, 1981

Remarks: This genus probably does not belong to the Heptacladidae, but to the entactinarian Triposphaeridae. However, the internal structure is not yet well known.

Paraheptacladus symmetricus
KOZUR & MOSTLER, 1981
(Pl. 8, Fig. 3)

1981 *Paraheptacladus symmetricus* n. sp. – KOZUR & MOSTLER, p. 27-28, Pl. 69, Fig. 1

Occurrence: Upper Anisian and Lower Ladinian of Austria, Hungary and Italy.

Genus *Welirella* DUMITRICĂ,
KOZUR & MOSTLER, 1980

Type species: *Welirella weveri* DUMITRICĂ, KO-ZUR & MOSTLER, 1980

Remarks: The assignment of *Welirella* to the Heptacladidae is tentative. The inner continuations of the main spines have (in their outer part) verticiles with three spines, like the Heptacladidae. However, the structure of the central part of the unit is unknown. Therefore we do not know, whether it has there an entactinarian spicular system or a microsphere.

Welirella fleuryi (DE WEVER, 1979,
in DE WEVER et al., 1979)
(Pl. 8, Fig. 10)

1979 *Conosphaera* (?) *fleuryi* DE WEVER, n. sp. – DE WEVER, SAN FILIPPO, RIEDEL & GRUBER, p. 78-79, Pl. 1, Figs. 5–7

Occurrence: Upper Anisian to Middle Carnian of the Tethys.

Remarks: *Welirella fleuryi* (DE WEVER, 1979) has 12 main spines with very broad base. In the holotype very big pores are present at the base of the main spines between their blades. However, these big pores may be closed by pore frames with smaller pores as in the paratype and in the present material.

Welirella mesotriassica n. sp.
(Pl. 8, Fig. 13)

1984 *Astrocentrus pulcher* KOZUR & MOSTLER, 1979 – LAHM, p. 20, Pl. 2. Fig. 5

Derivatio nominis: According the occurrence in the Middle Triassic

Holotypus: The specimen on Pl. 8, Fig. 13; rep.-no. KKM 1995/I-13.

Material: More than 100 specimens.

Diagnosis: *Welirella* with 14-15 main spines with broad blades and narrow deep furrows between them. Pores at the base of the spines moderately large.

Description: The spherical shell is double-walled. The outer pore frames surround large irregular pores and have nodes or short broad spines at the vertices. The inner pore frames enclose small oval or roundish pores. The 14-15 main spines have in their proximal part three high and broad blades that are separated by deep and narrow furrows. At their base, the blades have a median furrow. The pores at the base of the main spines are moderately large. The inner continuation of the main spines has vertices with three side spines.

Measurements:

Diameter of shell: 167–227

Length of main spines: 109–120

Width at the base of the main spines: 36–41

Occurrence: Illyrian to Ladinian of Austria, Hungary and Italy.

Remarks: LAHM (1984) assigned forms with double-layered shells to *Astrocentrus pulcher* KOZUR & MOSTLER, 1979, that has a spongy shell. According to his opinion the spongy character is caused by recrystallization. However, the Middle Carnian material from Göstling is excellently preserved and not recrystallized. It shows in all specimens of *Astrocentrus pulcher* a spongy shell. On the other hand, our material from the Weiße Wand Member is only moderately preserved and recrystallized but it shows clearly the double-layered character of the shell in *Welirella fleuryi* and *W. mesotriassica* with large outer pore frames and small inner pore frames.

Welirella fleuryi (DE WEVER, 1979) has only 12 main spines. Their blades are narrow and the furrows between them are broad. Therefore large pores are developed at the base of the spines at the place of the furrow between the blades. These large pore may be closed by the inner pore frames with small pores.

Welirella weveri DUMITRICĂ, KOZUR & MOSTLER, 1980 emend., has only 9 spines with a very broad base and very big pores at the base of the spines.

Family Pantanelliidae PESSAGNO, 1977

Genus *Pessagnollum* n. gen.

Type species: *Pessagnollum multispinosum* n. gen. n. sp.

Derivatio nominis: In honour of E.A. PESSAGNO, Dallas, for his outstanding contributions to the Mesozoic radiolarian research.

Diagnosis: The spherical shell has very large hexagonal and pentagonal pores and high pore frames. Two short, broad, pyramidal tricarinate polar spines and several smaller by-spines of similar shape are present that are concentrated to the equatorial plane.

Occurrence: Upper Illyrian of western Tethys.

Assigned species: *Pessagnollum multispinosum* n. gen. n. sp.

Remarks: The pore frames are typical for the Pantanelliidae. Very short polar spines are occasionally also present in *Ellipsoxiphus* DUNIKOWSKI, 1882 (junior synonyms: *Druppatractylus* HAECKEL, 1887, and *Pantanellium* PESSAGNO, 1977), e.g. in *Ellipsoxiphus* sp. aff. *P. haidaense* (PESSAGNO & BLOME, 1980), but this genus has no additional spines almost of the same size as the polar spines.

Pessagnollum multispinosum n. gen. n. sp.
(Pl. 8, Fig. 11)

Derivatio nominis: According to the numerous spines for the family Pantanelliidae.

Holotypus: The specimen on Pl. 8, Fig. 11; rep.-no. KKM 1995/I-10.

Material: 11 specimens.

Diagnosis: As for the genus.

Description: The spherical shell has the typical Pantanelliidae pore frames with very large hexagonal and pentagonal pores. The two polar spines are very short, broad, of pyramidal shape. They have

three high blades and very broad and deep furrows. Few vertices of the pore frames have short spines, but near the equatorial plane 6-8 short, broad, pyramidal spines are present that have about half of the size of the polar spines or are somewhat larger. The interior of all specimens is sediment filled preventing the observation of the inner structure, but a medullary shell is probably present.

Measurements:
Diameter of shell: 163–174 µm
Length of polar spines: 39–48 µm
Basal width of polar spines: 35-39 µm
Length of spines near the equatorial plane: 17–27 µm

Occurrence: *S. transitus* Zone (upper Illyrian) of Austria and Hungary.

Remarks: Pantanelliidae appear for the first time in the upper Olenekian, but are nearly absent in the Middle Triassic and become again common in the Norian. No species, similar to *P. multispinosum* is known.

Family Stylosphaeridae HAECKEL, 1882

Genus *Spongostylus* HAECKEL, 1882

Type species: *Spongostylus hastatus* HAECKEL, 1887

Spongostylus nakasekoi n. sp.
(Pl. 6, Fig. 18)

Derivatio nominis: In honour of Prof. KOJIRO NAKASEKO, Osaka, for his outstanding contributions to the radiolarian research in Japan.

Holotypus: The specimen on Pl. 6, Fig. 18; rep.-no. KKM 1995/I-15.

Material: 7 specimens, all with more or less corroded spongy shell.

Diagnosis: *Spongostylus* with very large, slightly twisted polar spines that are widest at the beginning of the distal third.

Description: The spherical spongy shell is badly fossilized. It consists of several densely spaced concentric spongy layers. The two polar spines are very large and slightly twisted. They are three-bla-

ded with wide and deep furrows. Their width increases slowly and continuously until the beginning of the distal third, where they are widest and decrease from there to the pointed distal end.

Measurements:
Diameter of shell: 115-140 µm
Length of polar spines: 257-285 µm
Maximum width of polar spines: 46-54 µm
Occurrence: Illyrian of Austria and Hungary.

Remarks: *Spongostylus nakasekoi* n. sp. is the forerunner of the Lower Ladinian *Spongostylus koppi* (LAHM, 1984). This species displays also slightly twisted large polar spines, but they become continuously narrower from their base to the pointed distal end.

Spongostylus tricostatus n. sp.
(Pl. 6, Fig. 16)

1990 *Spongopallium* cf. *koppi* (LAHM) – GORIČAN & BUSER, p. 157, Pl. 4, Figs. 2–4
1995 *Spongopallium* ? sp. RAMOVŠ & GORIČAN, Pl. 1, Figs. 6, 7

Derivatio nominis: According to the three-bladed polar spines.

Holotypus: The specimen on Pl. 6, Fig. 16; rep.-no. KKM 1995/I-7.

Material: 12 specimens.

Diagnosis: The spherical spongy shell has very big, three-bladed polar spines.

Description: The spherical shell is relatively small, spongy, consisting of numerous densely spaced spongy shells around a microsphere. The polar spines are long and very broad. They have three high blades, separated by deep, wide, V-shaped furrows. The proximal part of the polar spines is parallel sided or a slight widening occurs after the midlength. The distal narrowing to the pointed end occurs over a short distance.

Occurrence: *S. transitus* Zone (upper Illyrian) and Lower Ladinian of Austria and Slovenia.

Measurements:
Diameter of shell: 120–150 µm
Length of polar spines: 170–300 µm
Maximum width of the polar spines: 50–70 µm

Remarks: The Lower Ladinian *Spongostylus koppi* (LAHM, 1984) displays slender polar spines that become continuously narrower from their base to the pointed distal end. Specimens with slightly twisted slender polar spines occur also in our material, but in contrast to *S. koppi*, they are widest after their midlength. They may fit into the intraspecific variability of the new species, but it cannot be excluded that they are an independent taxon. They are assigned to *S.* cf. *tricarinata*.

GORIČAN & BUSER (1990) figured under *Spongopallium* ? cf. *koppi* forms that belong to the new species. The inner structure consisting of numerous densely spaced spongy shells around a tiny microsphere is well documented in this material. This is the typical structure of the Triassic *Spongostylus*, distinctly different from *Spongopallium* (see under Spongopalliidae).

Spongostylus ? *tetrapterus* (RAMOVŠ & GORIČAN, 1995) from the *S. transitus* Zone of Slovenia displays four-bladed polar spines. Its inner structure is unknown, but because of the similarity with *Spongostylus tricostatus* n. sp. it is rather a *Spongostylus* than a *Spongopallium*.

Genus *Staurolonche* HAECKEL, 1882

Type species: *Staurolonche robusta* RÜST, 1885

Staurolonche trispinosum trilobum (NAKASEKO & NISHIMURA, 1979)
(Pl. 10, Fig. 16)

1979 *Staurosphaera triloba* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 72, Pl. 5, Figs. 1, 2

1980 *Stauracontium* ? *trispinosum ladinicum* n. sp. – DUMITRICĂ, KOZUR & MOSTLER, p. 17, Pl. 1, Fig. 5 (?); Pl. 2, Fig. 4; Pl. 3; Figs. 6, 7; Pl. 5; Fig. 4; Pl. 14, Fig. 45

1990 *Stauracontium* ? *trispinosum* (KOZUR & MOSTLER), 1979 – GORIČAN & BUSER, p. 158, Pl. 1, Fig. 2

1990 *Stauracontium* ? *trispinosum ladinicum* DUMITRICĂ, KOZUR and MOSTLER – YEH, p. 20, Pl. 6, Fig. 17

Occurrence: Upper Anisian and Lower Ladinian of Japan, Philippines, Austria, Hungary, Italy, Slovenia.

Remarks: KOZUR & MOSTLER (1979) established *Staurosphaera trispinosa* for Middle Carnian forms, in which the lateral spines at the verticiles are as long as or longer than the proximal part of the main spines before the verticile. DUMITRICĂ, KOZUR & MOSTLER (1980) separated Ladinian forms, in which the lateral spines at the verticiles are distinctly shorter than the proximal part of the main spines before the verticile. For the same forms, NAKASEKO & NISHIMURA (1979) had established few month earlier *Staurolonche triloba*. Consequently, *S. trispinosum ladinicum* is a junior synonym of *S. triloba*. LAHM (1984) regarded *S. trispinosum ladinicum* as inseparable from *S. trispinosum trispinosum*, because transitional forms are present. GORIČAN & BUSER (1990) followed LAHM (1984), but they recognized the synonymy with *Staurosphaera triloba* (NAKASEKO & NISHIMURA, 1979).

Our studies have shown that in the Anisian only forms with short spines at the verticiles occur. In the Lower Ladinian these forms clearly dominate, but exceptionally already forms occur, in which the lateral spines at the verticiles are at least as long as the proximal part of the main spines before the verticile. In the Carnian only the latter forms are present. Therefore, a subdivision in subspecies level is furthermore possible.

One medullary shell is present. Consequently, the forms belong to *Staurolonche*, HAECKEL, 1882.

Staurolonche praegranulosa n. sp.
(Pl. 10, Fig. 11)

Derivatio nominis: According to the assumed ancestral position to *Staurolonche granulosa* (DUMITRICĂ, KOZUR & MOSTLER).

Holotypus: The specimen on Pl. 10, Fig. 11; rep.-no. KKM 1995/I-14.

Material: 7 specimens.

Diagnosis: The cortical shell has small trigonal to hexagonal pores. The four large main spines are slightly twisted and become continuously narrower from the base towards the pointed distal end.

Description: The spherical cortical shell displays pores of different size and shape. Triangular to hexagonal pores occur at one specimen. The four main spines are long, but differ somewhat in their length in one specimen. They are slightly twisted and tricarinate, in their distal part needle-like and round without blades and furrows. The furrows of the proximal part are deep and rather narrow. The main spines become continuously narrower from their relative broad base towards the pointed distal end.

Measurements:

Diameter of shell: 160–190 µm

Length of the main spines: 230–330 µm

Width of the main spines at their base: 50–70 µm

Occurrence: Illyrian of Austria and Hungary.

Remarks: In *Staurolonche granulosa* (DUMITRICĂ, KOZUR & MOSTLER, 1980) the proximal part is parallel-sided and nearly untwisted and the main spines are broadest at the beginning of the twisted distal part.

Family Spongopalliidae n. fam.

Diagnosis: Shell with two polar spines originating in an elongated inner medullary shell inside an elongated latticed shell (outer medullary shell) that is surrounded by a spongy mantle of various thickness.

Occurrence: Ladinian of western Tethys.

Assigned genus: *Spongopallium* DUMITRICĂ, KOZUR & MOSTLER, 1980.

Remarks: The Stylosphaeridae HAECKEL 1882, have no spongy mantle around a latticed medullary shell. If they have a spongy shell, like *Spongostylus* HACKEL, 1882, no latticed medullary shell is present surrounding the microsphere.

Genus *Spongopallium* DUMITRICĂ, KOZUR & MOSTLER, 1980

Type species: *Spongopallium contortum* DUMITRICĂ, KOZUR & MOSTLER, 1980

Spongopallium ? *tubulispina* n. sp.

1982   Spumellaria gen, et spec. indet. with tubular spines – DUMITRICĂ & MELLO, Pl. 2, Fig. 13

1990   *Spongopallium* ? sp. B – GORIČAN & BUSER, p. 158, Pl. 4, Fig. 6

Derivatio nominis: According to the tubular polar spines.

Holotypus: The specimen figured by GORIČAN & BUSER (1990, Pl. 4, Fig. 6); rep.-no. 87/220/7.

Locus typicus: Bohinj (northwestern Slovenia).

Stratum typicum: Limestone intercalation in tuffs and tuffites, sample 19726/5, middle part of Lower Ladinian (for locality and sample data see GORIČAN & BUSER (1990).

Diagnosis: *Spongopallium* (?) with tubular polar spines that are only distally carinate.

Description: The subspherical shell is spongy. The two polar spines have at their base several ridges and short, narrow furrows or pores between them. Then follows a tubular part and the distal part has sharp high blades separated by deep furrows that are connected with the hollow tube. The spines are widest at the beginning of the carinate distal part. Inner structure unknown.

Occurrence: Middle and Upper Fassanian of Italy, Slovakia and Slovenia.

Remarks: Our two present specimens were unsuccessfully broken for studying the inner structure. Therefore the well preserved specimen figured by GORIČAN & BUSER (1990, Pl. 4, Fig. 6) was chosen as holotype. The pore-bearing part at the base of the polar spines probably corresponds to the outer medullary shell and this part is not covered by the spongy mantle. By the tubular polar spine this species is well recognizable and easily separable from other *Spongopallium* species.

Superfamily Sponguracea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1981
Family Oertlispongidae KOZUR & MOSTLER
(in: DUMITRICĂ et al., 1980)

Genus *Paroertlispongus* KOZUR & MOSTLER, 1981

Type species: *Paroertlispongus multispinosus* KO-ZUR & MOSTLER, 1981

Paroertlispongus multispinosus KOZUR & MOSTLER, 1981
(Pl. 11, Fig. 12)

1981   *Paroertlispongus multispinosus* n. gen. n. sp. – KOZUR & MOSTLER, p. 48, Pl. 44, Fig. 2; Pl. 45, Fig. 1

1984   *Paroertlispongus multispinosus* KOZUR & MOSTLER, 1981 – LAHM, p. 45-46, Pl. 7, figs. 5, 6

1992   *Palaeoeucyrtis elongata* n. sp. – FENG, QINGLAI, Pl. 2, Fig. 13

1993   *Palaeoeucyrtis elongata* FENG, pars - FENG, QINGLAI & LIU, BENPEI, p. 548, Pl. 2, Figs. 1-3

1994   *Paroertlispongus multispinosus* KOZUR & MOSTLER, 1981 – KOZUR & MOSTLER, p. 69, Pl. 12, Fig. 10; Pl. 13, Figs. 4, 11

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian, uppermost Anisian) to Lower Ladinian of Austria, Hungary, Italy, China.

Remarks: *Paroertlispongus multispinosus* has a long main spine that become wider distalwards and is widest distinctly behind its midlength. Oertlispongidae are mostly preserved as isolated main spines. Most of the taxa can be determined by these spines and several taxa were established by isolated spines before the shell was known DUMITRICĂ (1982b). The shell is obviously not very resistant against dissolving in HF.

FENG, QINGLAI (1992) introduced the genus *Palaeoeucyrtis* FENG for such isolated spines of *Paroertlispongus* and for the isolated shorter spines of different Intermediellidae LAHM, 1994.

Family Intermediellidae LAHM, 1984

Genus *Paurinella* KOZUR & MOSTLER, 1981

Type species: *Paurinella curvata* KOZUR & MOST-LER, 1981

Synonym: *Yichunella* FENG, 1992

Paurinella fusina (FENG, 1992)
(Pl. 11, Fig. 10)

1992   *Palaeoeucyrtis fusina* n. sp. – FENG, QINGLAI, Pl. 2, Figs. 15, 16

1993   *Palaeoeucyrtis fusina* FENG – FENG, QINGLAI & LIU, BENPEI, p. 548–549, Pl. 2, Figs. 5–8

Occurrence: *S. transitus* Zone (upper Illyrian) of China, Austria and Hungary.

Remarks: FENG, QINGLAI (1992) and FENG, QINGLAI & LIU, BENPEI (1993) described isolated main spines of *Paroertlispongus* as well as of *Paurinella* and other Intermediellidae as *Palaeoeucyrtis*. The spindle-shaped isolated spines correspond in the form to the spines of an Upper Illyrian *Paurinella* species. FENG, QINGLAI (1992) and FENG, QINGLAI & LIU, BEN-PEI (1993) described also a *Paurinella* species, *P. sinensis*, that has partly the same spine type. The proximal tapering part of these spines is in general enclosed by the shell and cannot be observed in forms with preserved shell except, if the shell is corroded, as in our specimen on Pl. 11, Fig. 10.

Superfamily Trematodiscacea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1979
Family Relindellidae KOZUR & MOSTLER, 1980
(in: DUMITRICĂ et al., 1980)

Genus *Pentaspongodiscus* KOZUR & MOSTLER, 1979

Type species: *Pentaspongodiscus tortilis* KOZUR & MOSTLER, 1979

Pentaspongodiscus mesotriassicus
DUMITRICǍ, KOZUR & MOSTLER, 1980
(Pl. 4, Fig. 14)

1980   *Pentaspongodiscus mesotriassicus* n. sp. DUMITRICǍ, KOZUR & MOSTLER, p. 10, Pl. 8, Fig. 7

1984   *Pentaspongodiscus mesotriassicus* DUMITRICǍ, KOZUR & MOSTLER 1980 – LAHM, p. 56, Pl. 9, Fig. 11

1990   *Pentaspongodiscus mesotriassicus* DUMITRICǍ, KOZUR & MOSTLER, 1980 – GORIČAN & BUSER, p. 151, Pl. 2, Figs. 1, 2

Occurrence: *S. transitus* Zone (upper Illyrian) and Lower Ladinian of Austria, Hungary, Italy and Slovenia.

Remarks: *Pentaspongodiscus mesotriassicus* belongs to the most common species in the uppermost Anisian and above all in the Lower Ladinian of the western Tethys, but only in limestones samples. So far, this species was not discovered in radiolarites of the same age. Apparently, some radiolarian species cannot be well dissolved by HF from radiolarites.

Pentaspongodiscus steigeri LAHM, 1984
(Pl. 4, Fig. 15)

1984   *Pentaspongodiscus steigeri* n. sp. – LAHM, p. 56-57, Pl. 9, Fig. 12

Occurrence: *S. transitus* Zone (upper Illyrian) and Lower Ladinian of Austria, Hungary and Italy..

Suborder Nassellaria EHRENBERG, 1875
Family Sanfilippoellidae
KOZUR & MOSTLER, 1979

Synonym: Poulpinae DE WEVER, 1981

Genus *Neopylentonema* KOZUR, 1984

Type species: *Neopylentonema mesotriassica* KOZUR, 1984

Neopylentonema mesotriassica KOZUR, 1984
(Pl. 4, Fig. 11)

1984   *Neopylentonema mesotriassica* n. sp. – KOZUR, p. 71, Pl. 4, Fig. 5; Pl. 5, Fig. 1; Pl. 6, Fig. 1

1990   *Neopylentonema mesotriassica* KOZUR, 1984 – GORIČAN & BUSER, p. 148, Pl. 6, Fig. 11

Occurrence: Upper Anisian and Lower Ladinian of the western Tethys.

Genus *Poulpus* DE WEVER, 1979

Type species: *Poulpus piabyx* DE WEVER, 1979

Poulpus illyricus
KOZUR & MOSTLER, 1994
(Pl. 11, Fig. 9)

1994   *Poulpus illyricus* n. sp. KOZUR & MOSTLER, p. 117, Pl. 29, Figs. 8–10; Pl. 32, Figs. 1, 2, 4

Occurrence: Middle and upper Illyrian of Austria and Hungary.

Genus *Hozmadia*
DUMITRICǍ, KOZUR & MOSTLER, 1980

Type species: *Hozmadia reticulata* DUMITRICǍ, KOZUR & MOSTLER, 1980

Hozmadia rotunda
(NAKASEKO & NISHIMURA, 1979)
(Pl. 3, Figs. 3, 4, 6, 7, 8 [cf.], 10 [aff.], 11)

1979   *Tripilidium rotundum* NAKASEKO and NISHIMURA, n. sp. – NAKASEKO & NISHIMURA, p. 81–82, Pl. 8, Figs. 1-3

1982   *Hozmadia* (?) sp. A– YAO, Pl. 1, Fig. 15

1991   *Hozmadia* cf. *reticulata* DUMITRICǍ, KOZUR & MOSTLER, 1980 – BRAGIN, p. 97–98, Pl. 1, Fig. 7

1993 *Hozmadia rotunda* (NAKASEKO & NISHI-MURA) - SASHIDA, NISHIMURA, IGO, KAZA-MA & KAMATA, p. 84, Fig. 6-10

1994 *Hozmadia rotunda* (NAKASEKO & NISHI-MURA, 1979) - KOZUR & MOSTLER, p. 116, Pl. 29, figs. 3, 4, 7

1995 *Hozmadia rotunda* (NAKASEKO & NISHI-MURA, 1979) – RAMOVŠ & GORIČAN, p. 186, Pl. 7, Figs. 5-6

Occurrence: Middle and above all Upper Anisian of Austria, Hungary, Italy and Slovenia.

Remarks: The subspherical cephalis with large pentagonal pores, the curved feet that ends in a needle-like prolongation and the stout, pointed apical horn are characteristic features of *Hozmadia rotunda*. The form of the apical horn is variable. Partly it becomes continuously narrower towards the pointed distal end, partly the apical part is nearly parallel-sided or there is even a slight widening after the midlength and the distal part becomes rapidly narrower. In one specimen (Pl. 3, Fig. 10), the distal end of the apical spine is rounded. It may be a transition form to *Hozmadia rotundispina*. It is herein determined as *H*. aff. *rotunda*. Distinct nodes are in general present at the vertices of the pore frames, but few specimens (Pl. 3, Fig. 8) have a rather smooth surface. This may be preservation controlled. This form is determined as *H*. cf. *rotunda*.

Hozmadia latispinosa n. sp.
(Pl. 3, Figs. 1, 2)

Derivatio nominis: According to the very large apical horn.

Holotypus: The specimen on Pl. 3, Fig. 1; rep.-no. KKM 1995/I-16.

Material: 12 specimens.

Diagnosis: Cephalis spherical, with large pores. Apical horn very large, especially broad. Feet curved, rather broad, terminally without needle-like part.

Description: The cephalis is spherical and has a large aperture that is surrounded by a smooth brim. The pores are large, hexagonal or pentagonal and have high pore frames with nodes at the vertices.

The apical horn is very large, especially broad and in its largest part of the same width. It is widest a little behind the midlength and its width decreases only in the distal third. The distal end of the apical horn is pointed or slightly rounded and has no needle-like end. The three blades are very high, narrow and separated by very wide ad deep furrows. The three feet in prolongation of 2 L and D are slightly curved and have three high, narrow blades that reach until the pointed distal end that has no needle-like prolongation.

Measurements:
Length of the cephalis: 140–152 μm
Width of the cephalis: 140–155 μm
Lengths of the apical horn: 125–130 μm
Width at the midlenght of the apical horn: 56–60 μm
Length of the feet: 90–125 μm
Maximum width of the feet: 35 μm

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian) of the Weiße Wand Member (Loibl Formation), Austria.

Remarks: *Hozmadia rotunda* (NAKASEKO & NISHIMURA, 1979) has not so stout apical horn and the feet have a distal needle-like prolongation.

In *Hozmadia rotundispina* both the apical horn and the feet have round distal ends.

Hozmadia reticulocostata n. sp.
(Pl. 3, Fig. 9)

Derivatio nominis. According to the reticulate and costate surface of the cephalis.

Holotypus: The specimen on Pl. 3, Fig. 9; rep.-no. KKM 1995/I-17.

Material: 4 specimens.

Diagnosis: *Hozmadia* with large pores and costae that originate in the feet.

Description: The cephalis is spherical and has a large aperture that is surrounded by a narrow, smooth ring. The pores of the cephalis are large and have mainly pentagonal and tetragonal outline. Small nodes are present at the vertices of the pore frames. From the blades of the 2 feet L narrow costae run obliquely upward. The apical horn is large, tricarinate with high, narrow blades and

deep and wide furrows between them. The proximal part of the apical horn is nearly parallel-sided, the distal part tapers towards the pointed distal end. The three feet in prolongation of 2 L and D are curved, tricarinate and have a needle-like round distal portion.

Measurements:
Length of the cephalis: 120–130 µm
Width of the cephalis: 127–134 µm
Length of the apical horn: 105–116 µm
Width of the apical horn: 32–35 µm
Length of the feet: 70–85 µm
Width of the feet: 25–30 µm

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian) of the Weiße Wand Member (Loibl Formation), Austria.

Remarks: The similar *Hozmadia rotunda* (NAKASEKO & NISHIMURA, 1979) has no costae on the cephalis.

Hozmadia rotundispina n. sp.
(Pl. 2, Figs. 9-11; Pl. 3, Fig. 12)

Derivatio nominis: According to the rounded distal ends of the apical spine and feet.

Holotypus: The specimen on Pl. 3, Fig. 12; rep.-no. KKM 1995/I-18.

Material: 21 specimens.

Diagnosis: *Hozmadia* with large pores and broad apical spines and feet that have all a rounded distal end.

Description: The spherical cephalic has a large aperture surrounded by a smooth brim. The pores are large, mostly pentagonal and tetragonal. The large apical horn is broad, in the apical half parallel-sided, in the distal half slightly tapering towards the rounded distal end. The three blades are broad and have often in their basal part a median furrow. The furrows between the blades are deep and mostly narrow. The three feet in prolongation of 2 L and D are also broad, slightly curved to nearly straight. Their blades reach until the rounded distal end and often somewhat on the shell. They are sometimes broad and in this case the deep furrows are narrow, sometimes they are narrow and the deep furrows are broad.

Measurements:
Length of the cephalis: 127–150 µm
Width of the cephalis: 145–167 µm
Length of the apical horn: 107–130 µm
Width of the apical horn: 53–64 µm
Length of the feet: 100–130 µm
Width of the feet: 33–52 µm

Occurrence: *T. florida* Subzone of the *S. transitus* Zone (upper Illyrian) of the Weiße Wand Member (Loibl Formation), Austria.

Remarks: Most similar is *Hozmadia latispinosa* n. sp. that has, however, pointed distal ends of the apical spine and of the feet. Perhaps both forms are the end forms of a wide intraspecific variability.

Family Silicarmigeridae KOZUR & MOSTLER, 1980 (in: DUMITRICĂ et al., 1980)

Genus *Spongosilicarmiger* KOZUR, 1984

Type species: *Spongosilicarmiger italicus* KOZUR, 1984

Spongosilicarmiger nakasekoi YEH, 1990
(Pl. 1, Figs. 1-2, 6–10; Pl. 2, Figs. 1–3 [cf.])

1979   *Stichopterium* (?) sp. B – NAKASEKO & NISHIMURA, p. 80-81, Pl. 11, Figs. 2, 5

1990   *Spongosilicarmiger nakasekoi* YEH, n. sp. – YEH, p. 25, Pl. 5, Figs. 3, 16; Pl. 8, Figs. 4, 5; Pl. 9, Figs. 7, 8, 14; Pl. 11, Fig. 20

1995   *Spongosilicarmiger scabiturritus* SUGIYAMA, 1992 – RAMOVŠ & GORIČAN, 191, Pl. 6, Figs. 1-4

Occurrence: Upper Illyrian *S. transitus* Zone of Japan, Philippines, Austria, Hungary, Italy.

Remarks: The cephalis is covered by microgranular silica and therefore the pores are closed and also the pore frames are covered, but Sometimes the pores are open in the distal part of the cephalis. The smooth surface of the cephalis is the only difference to *Spongosilicarmiger scabiturritus* SUGIYAMA, 1992, with open pores and rugged surface as correctly mentioned by SUGIYAMA (1992). So-

metimes also in this species the pores are closed by recrystallization or an basal closure of microgranular silica. But also in such specimens the pore frames are visible and cause the rugged surface of the cephalis in S. *scabiturritus* . Consequently, the specimens with smooth cephalis surface that were assigned to S. *scabiturritus* by RAMOVŠ & GORIČAN (1995), belong to S. *nakasekoi*.

In *Spongosilicarmiger priscus* KOZUR & MOSTLER, 1994, the pores and pore frames of the cephalis are also closed by microgranular silica as in *S. nakasekoi*, but the surface of the cephalis is covered by distinct nodes and not smooth as in S. *nakasekoi*.

Spongosilicarmiger transitus laevis n. subsp.
(Pl. 1, Figs. 3, 4, 5, 11–13; Pl. 2, Figs. 5–7)

Derivatio nominis: According to the smooth cephalis.
Holotypus: The specimen on Pl. 1, Figs. 5, 11, 12; rep.-no. KKM 1995/I-19.
Material: 14 specimens.
Diagnosis: Cephalis smooth, poreless. Cephalic tube with coarse pore frames. Only a few pores are open the others are closed by microgranular silica. At least one foot strongly sidewards directed.
Description: The cephalis is moderately large, subspherical and poreless. It consists of dense, microgranular silica. Its surface is smooth and has few indistinct ribs. In the cephalic tube few roundish pores are open, but the pore frames are also visible around closed pores. The frustum-like postcephalic part has 5–6 narrow segments separated by narrow circumferential rings. The pores between the rings are roundish or irregular, but mostly closed. The aperture is large, open. The thorax feet are needle-like and in their upper part inserted in the shell, where they are visible as narrow ridges. They are strongly outward directed and connected by wing-like shell material except their distal part.
Measurements:
Length of the cephalic tube: 75–110 µm
Maximum width of the cephalic tube: 45–50 µm
Length of the cephalis: 55–75 µm

Width of the cephalis: 80–85 µm
Length of the postcephalic part of the test: 110–160 µm
Width of the postcephalic part of the test (without wings): 105–120 µm
Length of the feet: 140–180 µm
Occurrence: *T. florida* Subzone of *S. transitus* Zone (upper Illyrian) of Austria.
Remarks: *Spongosilicarmiger nakasekoi* YEH, 1990, is distinguished by the fewer outward direction of the feet.

In *Spongosilicarmiger transitus transitus* KOZUR & MOSTLER, 1994 from the upper *T. florida* Subzone and Y. annulata Subzone of the *S. transitus* Zone (upper Illyrian) the cephalis is covered by distinct nodes.

Spongosilicarmiger terebrus n. sp.
(Pl. 2, Figs. 4, 8, 12)

Derivatio nominis: According to the shape of the cephalotube.
Holotypus: The specimen on Pl. 2, Figs. 4, 8, 12; rep.-no. KKM 1995/I-20.
Material: 3 specimens.
Diagnosis: *Spongosilicarmiger* with blunt ending cephalotube that has at the distal end four short, cross-like arranged ribs and one or two intercalated ribs.
Description: Cephalis subspherical, covered with a layer of microgranular silica with a slightly uneven surface, but without open pores. Cephalic tube cylindrical with a blunt distal end that has 4 short cross-like arranged, high, narrow ribs and one or two intercalated ribs. These ribs cover only the blunt distal end that looks like a drill head. The remaining cephalotube has crater-like pore frames, but only few roundish pores are open. The frustum-like large postcephalic part of the test has five segments. The narrow and low circumferential rings are inserted in the shell and outside not well visible. The outer pore frames are well developed, but only some pores are open, mainly at both sides of the feet. The three feet in prolongation of D and 2 L are needle like and in the proximal part inserted in the shell, where they are visible as

narrow ridges. The distal, moderately outward directed part is free. The aperture is large, open.

Measurements:

Length of the cephalic tube: 80–90 µm

Maximum width of the cephalic tube: 40–44 µm

Length of the cephalis: 50–54 µm

Width of the cephalis: 76–85 µm

Length of the postcephalic part of the test: 105–125 µm

Width of the postcephalic part of the test: 100–110 µm

Length of the feet: Up to 200 µm

Occurrence: *T. florida* Subzone of *S. transitus* Zone (upper Illyrian) of Austria.

Remarks: The drill-head like, blunt, costate distal end of the cephalotube distinguishes this species from all other *Spongosilicarmiger* species.

7. Stratigraphic evaluation of the radiolarian fauna (see table 1)

KOZUR & MOSTLER (1994) recognized the very big differences between the radiolarian faunas of the Illyrian (Upper Anisian) *Paraceratites trinodosus* ammonoid Zone (*T. laevis* radiolarian zone) and the Fassanian *Reitziites reitzi* ammonoid Zone (*S. italicus* radiolarian zone). These differences were so strong that many guide forms of the S. italicus Zone are not directly related to ancestors in the *T. laevis* Zone. This very sharp change between the Upper Anisian and Lower Ladinian radiolarian fauna in a short stratigraphic interval had the disadvantage that many Ladinian forms appeared without ancestor in the next older radiolarian zone. Moreover, it was to expect that still a radiolarian fauna between the *T. laevis* and *S. italicus* zones was present. This fauna was now contemporaneously found in Slovenia (RAMOVŠ & GORIČAN, 1995) and in the southern Karawanken (present paper). It represents the *T. florida* Subzone of the *S. transitus* Zone (Kozur, 1995) between the *T. laevis* and *S. italicus* Zone. Not so rich assemblages of this fauna were known since NAKASEKO & NISHIMURA (1979), but except KOZUR & MOSTLER (1994) and RAMOVŠ & GORIČAN (1995)

these faunas were either incorrectly or not exactly dated. One of these faunas is the *Tiborella florida* fauna of Japan that was dated by NAKASEKO & NISHIMURA (1979) as Upper Triassic. This dating again was used to date taxa similar to species of this assemblage as possible Carnian (YEH, 1990, p. 25). Both KOZUR & MOSTLER (1994) and RAMOVŠ & GORIČAN (1995) dated this fauna as latest Anisian near the Anisian-Ladinian boundary (defined with the base of the *Reitziites reitzi* ammonoid zone s.str.).

The similar, but at least partly a subzone younger *Busuanga chengi* assemblage (*Y. annulata* Subzone of the *S. transitus* Zone sensu KOZUR, 1995) of latest Anisian age was assigned to the Ladinian by YEH (1990).

A part of the radiolarian faunas described by MARTINI et al. (1989) and DE WEVER et al. (1990) belongs also to the *S. transitus* Zone. Another part of these radiolarian faunas with *Tetraspinocyrtis laevis* belongs to the Upper Anisian *T. laevis* Zone and parts of these faunas with *Oertlispongus inaequispinosus* belongs to the Lower Ladinian. Thus, the summarizing assignment of these faunas as Anisian-Ladinian was correct, but not precise.

FENG, QINGLAI (1992) and FENG, QINGLAI & LIU BENPEI (1993) assigned the *"Shengia yini"* assemblage to the lowermost Scythian and the *"Pseudoeucyrtis liui"* assemblage to the Upper Scythian. Both are typical radiolarian faunas of the *S. transitus* Zone and belong because of the occurrence of *Triassocampe scalaris* DUMITRICĂ, KOZUR & MOSTLER, 1980 (= *Triassocampe soror* FENG & LIU, 1993 and *Shengia nanpanensis* FENG, 1992) to their largest part to the upper subzone (*Y. annulata* Subzone) of the *S. transitus* Zone. *Pseudoeucyrtis liui* FENG 1992 is an *Archaeospongoprunum mesotriassicum* KOZUR & MOSTLER, 1981 that is a typical upper Anisian guideform. Its co-occurrence with *Triassocampe deweveri* (NAKASEKO & NISHIMURA) (= *Shengia solida* FENG) and *T. scalaris* indicates the latest Anisian upper subzone (*Y. annulata* Subzone) of the *S. transitus* Zone for the "*Pseudoeucyrtis liui* assemblage". The same age is indicated for the upper *"Shengia yini* assemblage", in which *T. scalaris* is already common, but also in the lower

part of this assemblage *T. soror* (= *T. scalaris*) is rarely present. There also *T. deweveri* (= *Shengia solida*) is rarely present and *Paurinella fusina* (FENG) is common that occurs also in the *T. florida* Subzone of the *S. transitus* Zone of Austria. Thus, apparently the lower part of the "*Shengia yini* assemblage" belong to the *T. florida* Subzone or to the lower part of the *Y. annulata* Subzone of the *S. transitus* Zone.

Our rich fauna makes it now easier to recognize the *T. florida* Subzone (and the *S. transitus* Zone in general) also in faunas, in which *T. florida* is absent. Characteristic for the *T. florida* Subzone (and the *S. transitus* Zone in general) is the dominance of Anisian elements that range up from the *T. laevis* Zone together with the first Ladinian elements and some forms that are restricted to the *S. transitus* Zone or the *T. florida* Subzone. Important and common species that ranges up from the *T. laevis* Zone (or older zones) and do no more occur in the *S. italicus* Zone are: *Eptingium manfredi japonicum, E. nakasekoi, E. ramovsi, Hindeosphaera spinulosa, Hozmadia costata, Parasepsagon variabilis, Parentactinia lata, Pentactinocapsa awaensis, Pentactinorbis dumitricai, Pseudosepsagon ? anisicus, Pseudosepsagon pentaspinosus, P. compacta, P. japonica, Silicarmiger costatus anisicus, Spongostephanidium japonicum, S. longispinosum, Tiborella florida austriaca, Weverisphaera anisica, Acanthosphaera carterae, Acanthosphaera nicorae, Hozmadia rotunda* and *Poulpus illyricus.* With exception of the last 4 species (Spumellaria and Nassellaria) these are all Entactinaria, the dominant element of the Anisian faunas.

Species, restricted to the *S. transitus* Zone (S.t.), *T. florida* Subzone (T.f.) or to the *Yeharaia annulata* Subzone (Y.a.) are: *Hexatortilisphaera aequispinosa* (S.t.), *Hexatortilisphaera bipolaris* (S.t.), *Pentactinocapsa multispinosa* (S.t.), *Pseudostylosphaera goricanae* (S.t.), *Tiborella florida florida* (T.f.), *Triassistephanidium anisicum* (T.f.), *Heptacladus ? anisicus* (S.t.), *Livinallongella lahmi* (S.t.), *Paurinella fusina,* (S.t.), *Paurinella sinenesis* (S.t.), *Pessagnollum multispinosum* (T.f.), *Pseudoertlispongus angulata* (Y.a.), *Spongostylus tricostatus* (S.t.), *Spongostylus nakasekoi*

(S.t.), *Spongostylus tetrapterus* (S.t.), *Staurolonche praegranulosa* (S.t.), *Hozmadia latispinosa* (S.t.), *H. reticulocostata* (S.t.), *H. rotundispina* (S.t.), *Spongosilicarmiger nakasekoi* (S.t.), *Spongosilicarmiger transitus laevis* (T.f.), *Spongosilicarmiger terebrus* (T.f.) and *Triassocampe scalaris baloghi* (Y.a.). Several of these forms are rare and may have a longer range beyond the *S. transitus* Zone. Especially an occurrence in older zones cannot be excluded for several of these species because they begin without known ancestral form. On the other hand, several of these species have their successors in the following Lower Ladinian *S. italicus* Zone. Consequently, most of the species of this group have at least their uppermost occurrence in the *T. transitus* Zone. However, *Paurinella fusina, P. sinensis* and *Pseudoertlispongus angulata* are species of typical Lower Ladinian genera that began in the *S. transita* Zone, and *T. scalaris baloghi* is a subspecies of a typical Lower Ladinian species.

A third stratigraphically important group are taxa that begin at the base or within the *S. transitus* Zone, but ranges at least into the following Lower Ladinian *S. italicus* Zone. These species are: *Eptingium manfredi manfredi, Pseudoertlispongus mostleri* (begins in the *Y. annulata* Subzone), *Triassocampe deweveri, T. scalaris scalaris* (begins in the *Y. annulata* Subzone), *Triassospongocyrtis longispinosa, Yeharaia annulata* (begins in the *Y. annulata* Subzone).

All other species of the *S. transitus* Zone are long-ranging forms or extraordinary rare forms with unknown range.

From the above list is clearly recognizable that in the *S. transitus* Zone the Anisian forms clearly dominate. These forms disappeared at the base of the overlying *S. italicus* Zone. Many characteristic Ladinian forms, such as Oertlispongidae with recurved or otherwise differentiated main spine that are very characteristic for the overlying *S. italicus* and younger Ladinian zones, are totally missing. Few taxa are restricted to the *T. florida* Subzone. The *Y. annulata* Subzone is distinguished from the *T. florida* Subzone by the appearance of a few further Ladinian species, *Pseudoertlispongus mostleri, Triassocampe scalaris* and *Yeharaia annulata..*

Krainer & Mostler (1992) and Kozur & Mostler (1994)						Kozur (1995) and present paper)					
Stage	Substage	Ammonoid Zone/Subzone	Conodont Zone	Radiolarian Zone	Rad. Subzone	Stage	Substage	Ammonoid Zone/Subzone	Conodont Zone	Radiolarian Zone	Rad. Subzone
Ladinian	Fassanian	*Eoprotrachyceras curionii*	*B. truempyi*	unnamed	unnamed	Ladinian	Fassanian	*Eoprotrachyceras curionii*	*B. truempyi*	unnamed	unnamed
		Nevadites fauna	*Neogondolella transita*	*Ladinocampe multiperforata*	*Ladinocampe vicentinensis*			*Nevadites secedensis*	*P. ? trammeri – Neogondolella transita*	*Ladinocampe multiperforata*	*Ladinocampe vicentinensis*
					Ladinocampe annuloperforata						*Ladinocampe annuloperforata*
		"*Xenopro-trachyceras*" *reitzi* — *Halilucites costosus*	*Neogondolella mesotriassica – Paragondolella? trammeri praetrammeri*	*Spongosilicar-miger italicus*	*O. inaequispinosus*			*Reitziites reitzi* — *Halilucites costosus*	*Paragondolella alpina – Paragondolella? trammeri*	*Spongosilicar-miger italicus*	*O. inaequispinosus*
		Reitziites reitzi			*Oertilispongus primitivus*			*Reitziites reitzi*			*Oertilispongus primitivus*
		Kellnerites felsoeoers.			*Spongosilicarmiger transitus*	Anisian	Illyrian	*Kellnerites felsoe-oersensis* — *Kellnerites felsoeoers.*	*Neogondolella mesotriassica*	*Spongosilicar-miger transitus*	*Yeharaia annulata*
								Lardaro-ceras pseudohung.			*Tiborella florida*
Anisian	Illyrian	not investigated	not investigated	not investigated	not investigated						
		Paraceratites trinodosus	*Neogondolella constricta*	*Tetraspinocyrtis laevis*				*Paraceratites trinodosus*	*Neogondolella constricta*	*Tetraspinocyrtis laevis*	

Table 1: Comparison of the ammonoid, conodont, and radiolarian zonation by KRAINER & MOSTLER (1992), KOZUR & MOSTLER (1994) with that by KOZUR (1995) and present paper.

Some Anisian forms become very rare or disappeared, such as *Parentactinia* lata, *Pentactinocapsa awaensis* and *Spongosilicarmiger nakasekoi*. Despite the fact that also in the *Y. annulata* Subzone the species dominance of the Anisian forms continued, the few Ladinian forms become already rich in specimens. By this, the *Y. annulata* Subzone has transitional character between Upper Anisian and Lower Ladinian radiolarian faunas, but forms of Anisian character are still dominant.

At the base of the *S. italicus* Zone (base of the *Reitziites reitzi* ammonoid zone) the Ladinian forms dominate both in the number of taxa and in specimens. This is caused both by disappearance of Anisian forms and above all by appearance of numerous Ladinian species and genera. For this reason, the radiolarians favours the priority Ladinian base at the base of the *R. reitzi* Zone s.str. (= base of the *S. italicus* Zone).

Acknowledgements

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Authors' addresses:
Dr. sc. Heinz W. Kozur, Rézsü u. 83, H-1029 Budapest, Hungary; Doz. Dr. Karl Krainer, Univ.-Prof. Dr. Helfried Mostler, Institute of Geology and Paleontology, University of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria.

Explanation of Plates

All figured specimens are from the Weiße Wand Member (Loibl Formation) of the locality Weiße Wand in the Southern Karawanken, Austria (see Text-Figs. 1, 3). They all belong to the *Tiborella florida* Subzone of the *Spongosilicarmiger transitus* Zone (upper Illyrian, uppermost Anisian)

Plate 1

Figs. 1, 2, 6–10: *Spongosilicarmiger nakasekoi* YEH, 1990, sample WW 7; Figs. 1, 2, 6, 7, 9: different views and magnifications of one specimen, rep.-no. KKM 1995/I-88, Figs. 1, 2: x 200, different views, Fig. 6: x 129, Figs. 7, 9: different view of proximal part, x 500; Figs. 8, 10: different magnifications of a distally broken specimen, rep.-no. KKM 1995/I-35, Fig. 8: x 155, Fig. 10: x 200.

Figs. 3–5, 11–13: *Spongosilicarmiger transitus laevis* n. subsp., sample WW 12, Figs. 3, 4: different views of the same specimen, various degree of outward direction of the feet well recognizable, x 200, rep.-no. KKM 1995/I-33; Figs. 5, 11, 12: holotype, rep.-no. KKM 1995/I-19, Fig. 5: detail of proximal part, x 500, Figs. 11, 12: different views of the entire specimen, x 200; Fig. 13, x 200, rep.-no. KKM 1995/I-34.

Plate 2

Plate 3

Figs. 1, 2:   *Hozmadia latispinosa* n. sp., sample WW 9, x 200; Fig. 1: holotype, rep.-no. KKM 1995/I-16; Fig. 2; rep.-no. KKM 1995/I-24.

Figs. 3, 4, 6, 7, 11: *Hozmadia rotunda* (NAKASEKO & NISHIMURA, 1979), sample WW 8, rep.-no. KKM 1995/I-25; Figs. 3, 4: x 200; Fig. 6: x 145; Fig. 7. x 160; Fig. 11: x 140.

Figs. 5, 13-16:   *Tiborella florida florida* (NAKASEKO & NISHIMURA, 1979), x 200; Fig. 5: sample WW 6, KKM 1995/I-26; Fig. 13: sample WW 8, rep.-no. KKM 1995/I-27 ; Fig. 14: sample WW 9, rep.-no. KKM 1995/I-28: Fig. 15: sample WW 12, rep.-no. KKM 1995/I-29; Fig. 16. sample WW 13, rep.-no. KKM 1995/I-30.

Fig. 8:   *Hozmadia* cf. *rotunda* (NAKASEKO & NISHIMURA, 1979), x 145, sample WW 9, rep.-no. KKM 1995/I-36.

Fig. 9:   *Hozmadia reticulocostata* n. sp., holotype, x 200, sample WW 13, rep.-no. KKM 1995/I-17

Fig. 10:   *Hozmadia* aff. *rotunda* (NAKASEKO & NISHIMURA, 1979), x 145, sample WW 9, rep.-no. KKM 1995/I-37.

Fig. 12:   *Hozmadia rotundispina* n. sp., holotype, x 125, rep.-no. KKM 1995/I-18.
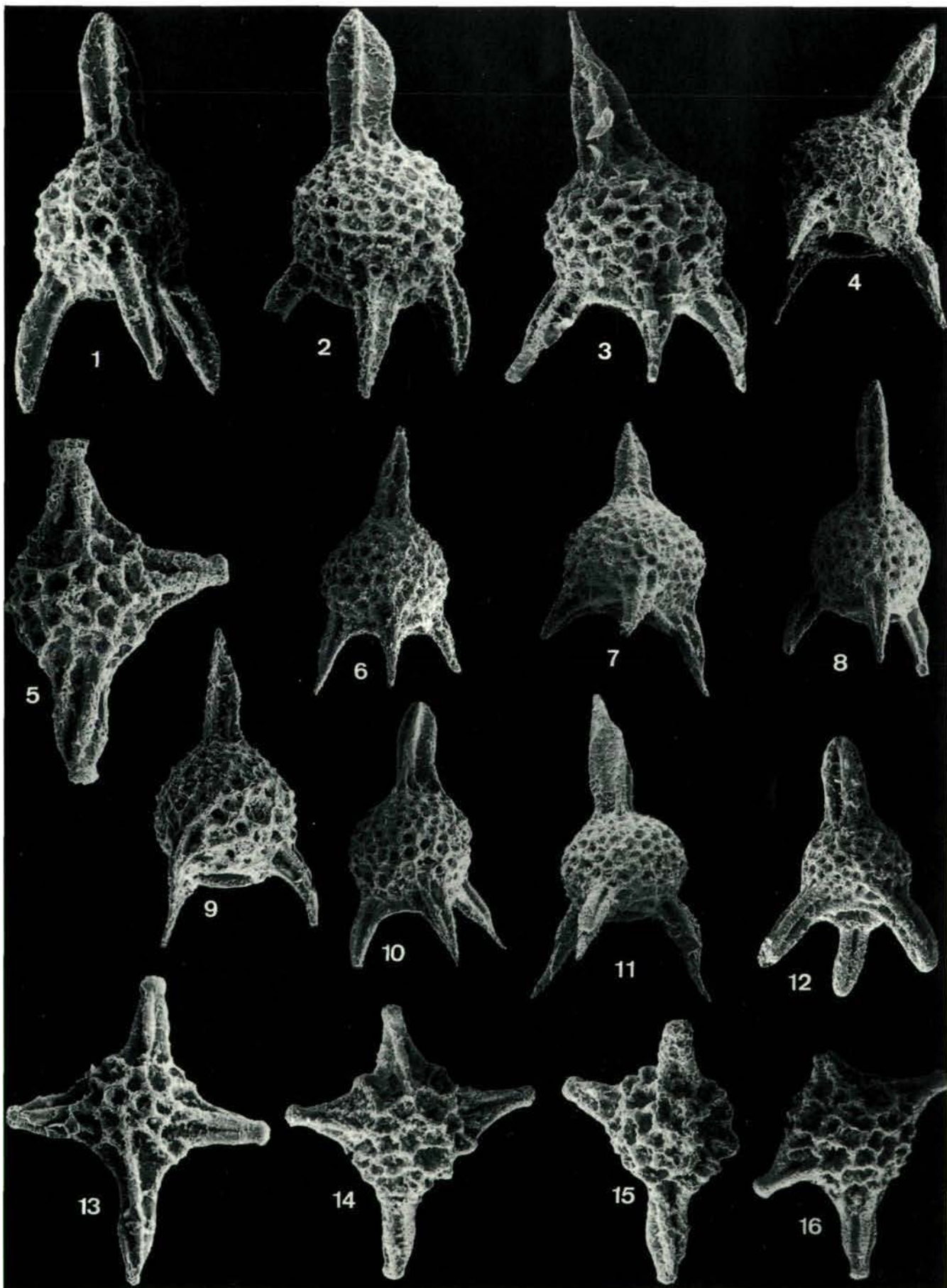
Plate 4

Figs. 1, 5:   *Tiborella florida austriaca* n. sp., x 200, sample WW 6; Fig. 1: holotype, rep.-no. KKM 1995/I-1; Fig. 5: rep.-no. KKM 1995/I-38.

Figs. 2, 3, 7, 9:   *Parasepsagon variabilis* (NAKASEKO & NISHIMURA, 1979), x 200; Fig. 2: sample WW 6, rep.-no. KKM 1995/I-38; Fig. 3: sample WW 8, rep.-no. KKM 1995/I-39; Fig. 7: sample WW 9, rep.-no. KKM 1995/I-40; Fig. 9: sample WW 12, rep.-no. KKM 1995/I-41.

Figs. 4, 8:   *Hindeosphaera spinulosa* (NAKASEKO & NISHIMURA, 1979); Fig. 4: x 170, sample WW 7, rep.-no. KKM 1995/I-42; Fig. 8: x 180, sample WW 12, rep.-no. KKM 1995/I-42.

Fig. 6, 10:   *Pseudosepsagon* ? *anisicus* (KOZUR & MOSTLER, 1994), x 200; Fig. 6: doubtful specimen with atypical position of the spines, sample WW 8, rep.-no. KKM 1995/I-43; Fig. 10: sample WW 6, rep.-no. KKM 1995/I-44.

Fig. 11:   *Neopylentonema mesotriassica* KOZUR, 1984, x 230, sample WW 13, rep.-no. KKM 1995/I-45.

Fig. 12:   Broken, indeterminable, probably four-spined entactinarian or spumellarian Radiolaria, x 200, sample WW 12, rep.-no. KKM 1995/I-46.

Fig. 13:   *Eptingium ramovsi* n. sp., x 200, sample WW 7, rep.-no. KKM 1995/I-47.

Fig. 14:   *Pentaspongodiscus mesotriassicus* DUMITRICĂ, KOZUR & MOSTLER, 1980, x 100, sample WW 6, rep.-no. KKM 1995/I-48.

Fig. 15:   *Pentaspongodiscus steigeri* LAHM, 1984, x 100, sample WW 12, rep.-no. KKM 1995/I-49.
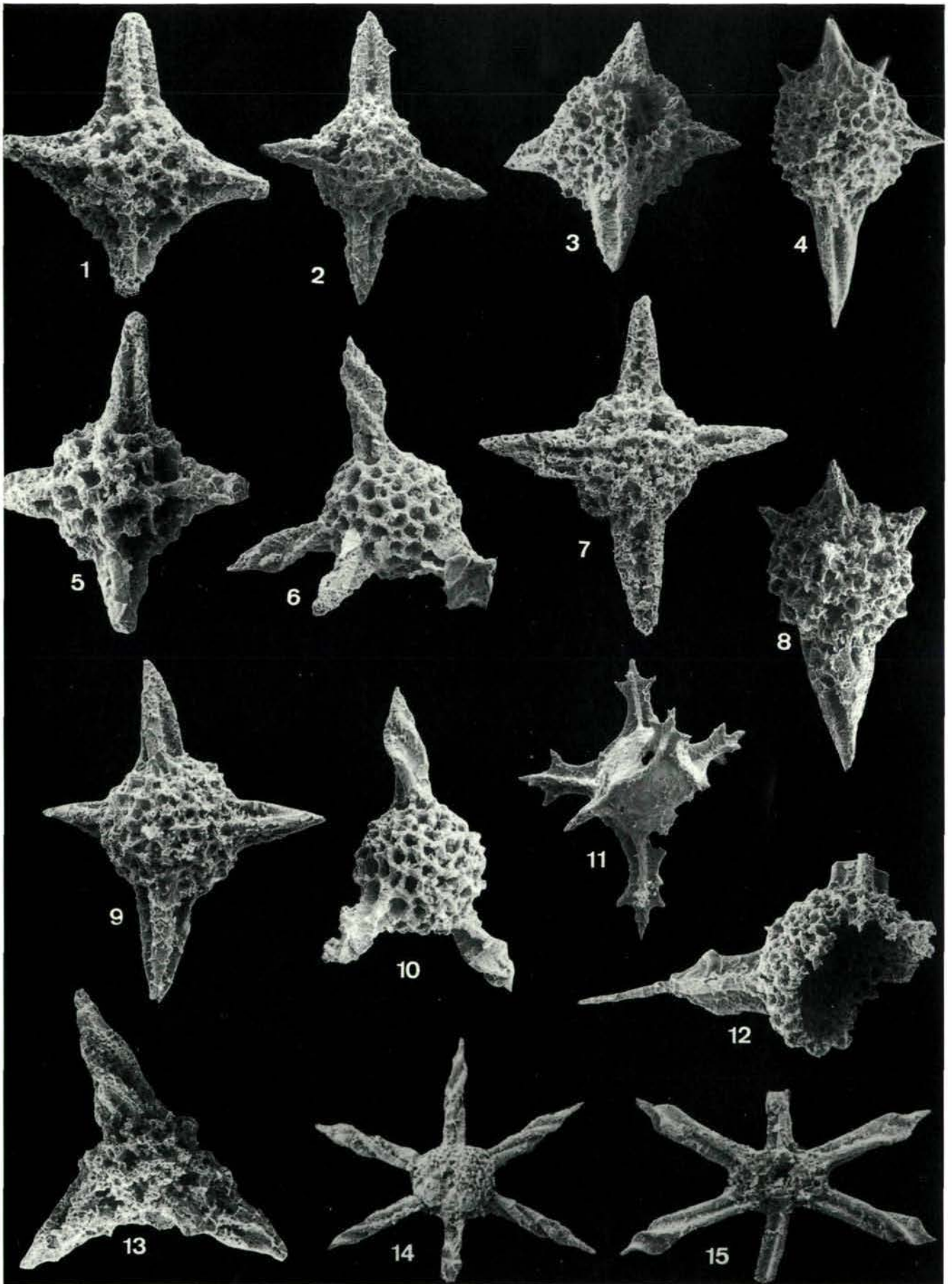
Plate 5

Figs. 1–10, 12: *Pentactinocapsa multispinosa* n. sp., x 200; Fig 1: lateral view, sample WW 3, rep.-no. KKM 1995/I-50; Fig. 2: oblique lateral-upper view, sample WW 1, rep.-no. KKM 1995/I-51; Fig. 3: lateral view, sample WW 4, rep.-no. KKM 1995/I-52; Fig. 4: lateral view, sample WW 6, rep.-no. KKM 1995/I-53; Fig. 5: somewhat oblique lateral view, sample WW 7, rep.-no. KKM 1995/I-54; Fig. 6: upper view, sample WW 7, rep.-no. KKM 1995/I-55; Fig. 7: lateral view, sample WW 8, rep.-no. KKM 1995/I-56; Fig. 8: upper view, sample WW 9, rep.-no. KKM 1995/I-57; Fig. 9: upper view, sample WW 9, rep.-no. KKM 1995/I-58; Fig. 10: somewhat oblique upper view, sample WW 12, rep.-no. KKM 1995/I-59; Fig. 12: oblique lateral-upper view, sample WW 13, rep.-no. KKM 1995/I-60.

Fig. 11: *Pentactinocapsa awaensis* (NAKASEKO & NISHIMURA, 1979), somewhat oblique lateral(-lower) view, x 140, rep.-no. KKM 1995/I-61.
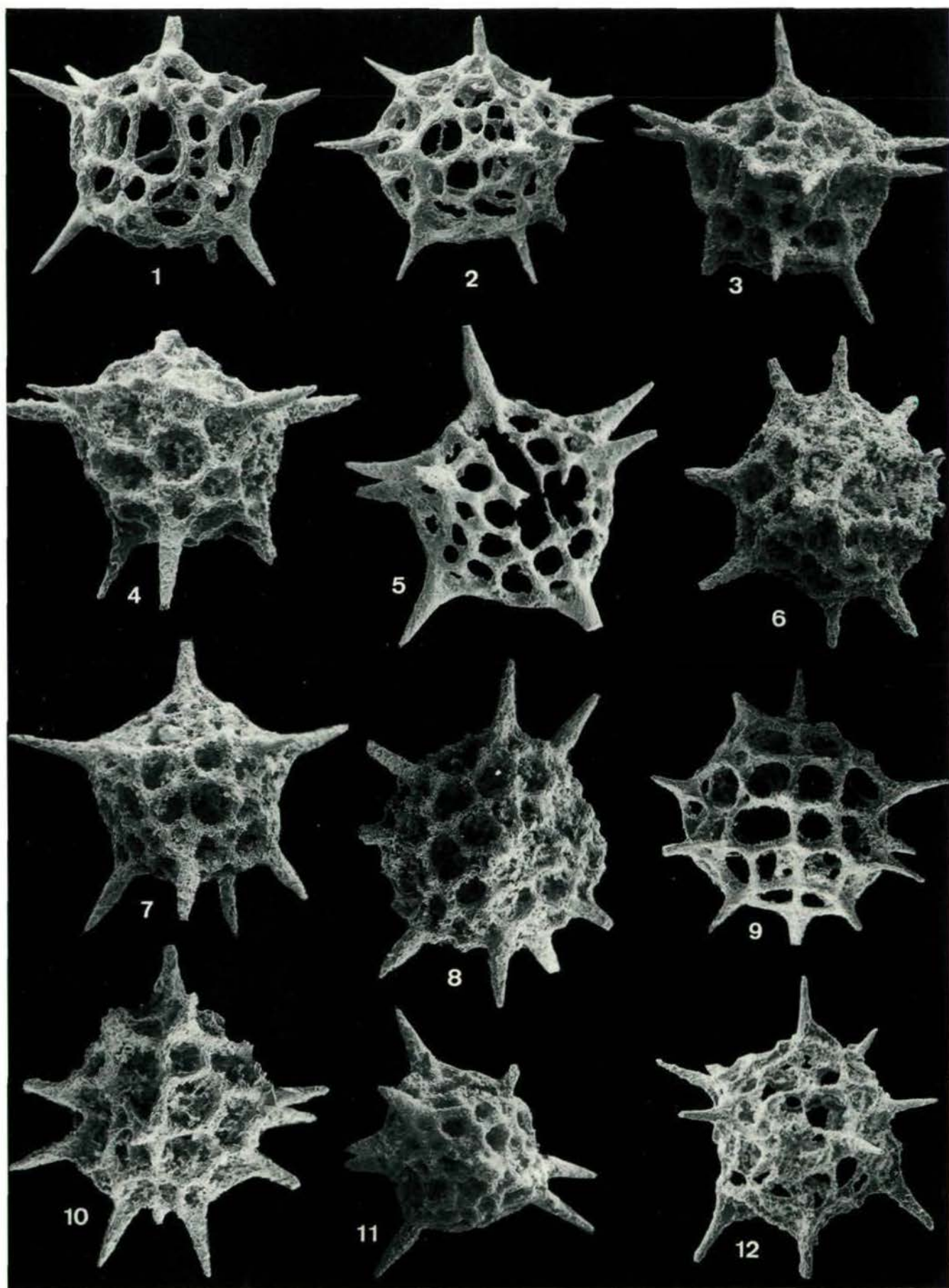
Plate 6

Figs. 1–3:   *Spongostephanidium japonicum* (NAKASEKO & NISHIMURA, 1979), Fig. 1: x 180, sample WW 4, rep.-no. KKM 1995/I-62; Fig. 2: x 200, sample WW 8, rep.-no. KKM 1995/I-63; Fig. 3: x 200, sample WW 6, rep.-no. KKM 1995/I-64.

Figs. 4, 5, 6 ?,   *Spongistephanidium longispinosum* SASHIDA, 1991; Fig. 4: x 220, sample WW 3, rep.-no. KKM
8 ?, 11 ?:5:   1995/I-65; Fig. 5 x 230, sample WW 6, rep.-no. KKM 1995/I-66; Fig. 6: x 200, sample WW 9, rep.-no. KKM 1995/I-67; Fig. 8: somewhat oblique lateral-equatorial view of a specimen with basally unusually broad spines that is only tentatively assigned to *S. longispinosum*, x 240, rep.-no. KKM 1995/I-68; Fig. 11: specimen with unusual asymmetric spine position, x 230, sample WW 7, rep.-no. KKM 1995/I-69.

Figs. 7, 9:   *Spongostephanidium austriacum* n. sp., Fig. 7: x 250, sample WW 8, rep.-no. KKM 1995/I-70; Fig. 9: holotype, x 230, sample WW 7, rep.-no. KKM 1995/I-4.

Fig. 10:   Eptingiidae DUMITRICĂ, 1978, n. gen. n. sp., x 240, sample WW 12, rep.-no. KKM 1995/I-71.

Figs. 12-14:   *Pseudostylosphaera coccostyla acrior* (BRAGIN, 1986); Fig. 12: x 145, sample WW 4, rep.-no. KKM 1995/I-72; Fig. 13: x 140, sample WW 3, rep.-no. KKM 1995/I-73; Fig. 14: x 145, sample WW 12, rep.-no. KKM 1995/I-74.

Fig. 15:   *Pseudostylosphaera japonica* (NAKASEKO & NISHIMURA, 1979), x 200, sample WW 9, rep.-no. KKM 1995/I-76.

Fig. 16:   *Spongostylus tricostatus* n. sp., holotype, x 170, sample WW 3, rep.-no. KKM 1995/I-7.

Fig. 17:   *Pseudostylosphaera compacta* (NAKASEKO & NISHIMURA, 1979) emend., x 110, sample WW 8, rep.-no. KKM 1995/I-75.

Fig. 18:   *Spongostylus nakasekoi* n. sp., holotype, x 130, sample WW 9, rep.-no. KKM 1995/I-15.
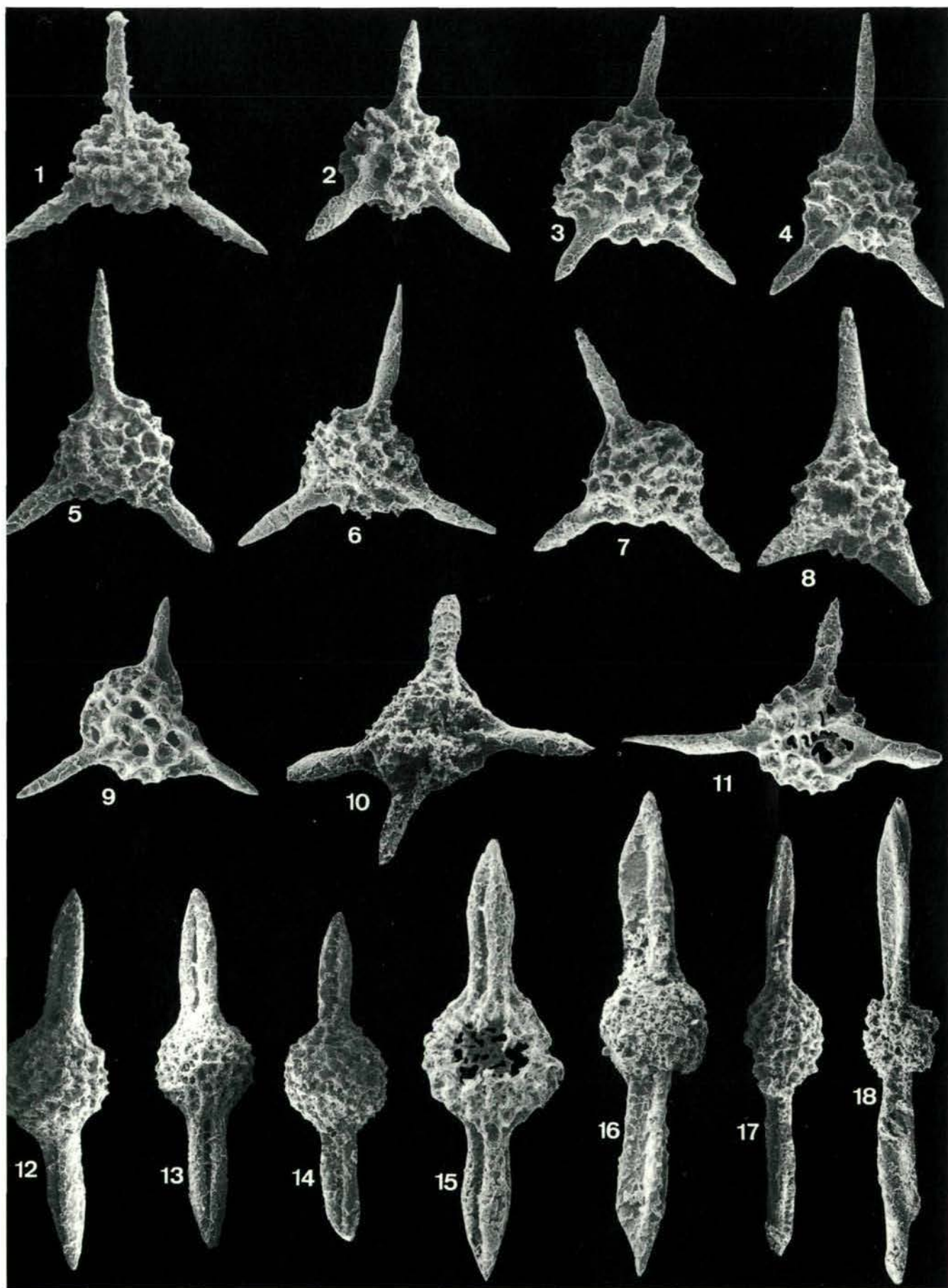
Plate 7

Figs. 1, 2, 4, 5, 7: *Livinallongella lahmi* n. sp.; Fig. 1: x 130, sample WW 12, rep.-no. KKM 1995/I-81; Fig. 2: holotype, x 140, sample WW 12, rep.-no. KKM 1995/I-6; Fig. 4: x 150, sample WW 13, rep.-no. KKM 1995/I-82; Fig. 5: x 150, sample WW 12, rep.-no. KKM 1995/I-83; Fig. 7: x 170, sample WW 12, rep.-no. KKM 1995/I-84.

Fig. 3, 6: *Livinallongella* cf. *lahmi* n. sp.; Fig. 3: x 140, sample WW 12, rep.-no. KKM 1995/I-86; Fig. 6: x 150, sample WW 13, rep.-no. KKM 1995/I-87.

Fig. 8: *Livinallongella* aff. *lahmi* n. sp., x 125, sample WW 12, rep.-no. KKM 1995/I-85.

Fig. 9: *Helioentactinia oertlii* (KOZUR & MOSTLER, 1979), x 80, sample WW 3, rep.-no. KKM 1995/I-76.

Figs. 10, 11, *Heptacladus* ? *anisicus* n. sp.; Fig. 10: holotype, x 120, sample WW 6, rep.-no. KKM 1995/I-5; Fig. 11: x 110,

13, 14: sample WW 8, rep.-no. KKM 1995/I-78; Fig. 13: x 150, sample WW 7, rep.-no. KKM 1995/I-79; Fig. 14: x 150, sample WW 12, rep.-no. KKM 1995/I-80.

Fig. 12: *Heptacladus crassispinus* DUMITRICĂ, Kozur & MOSTLER, 1980, x 120, sample WW 7, rep.-no. KKM 1995/I-77.
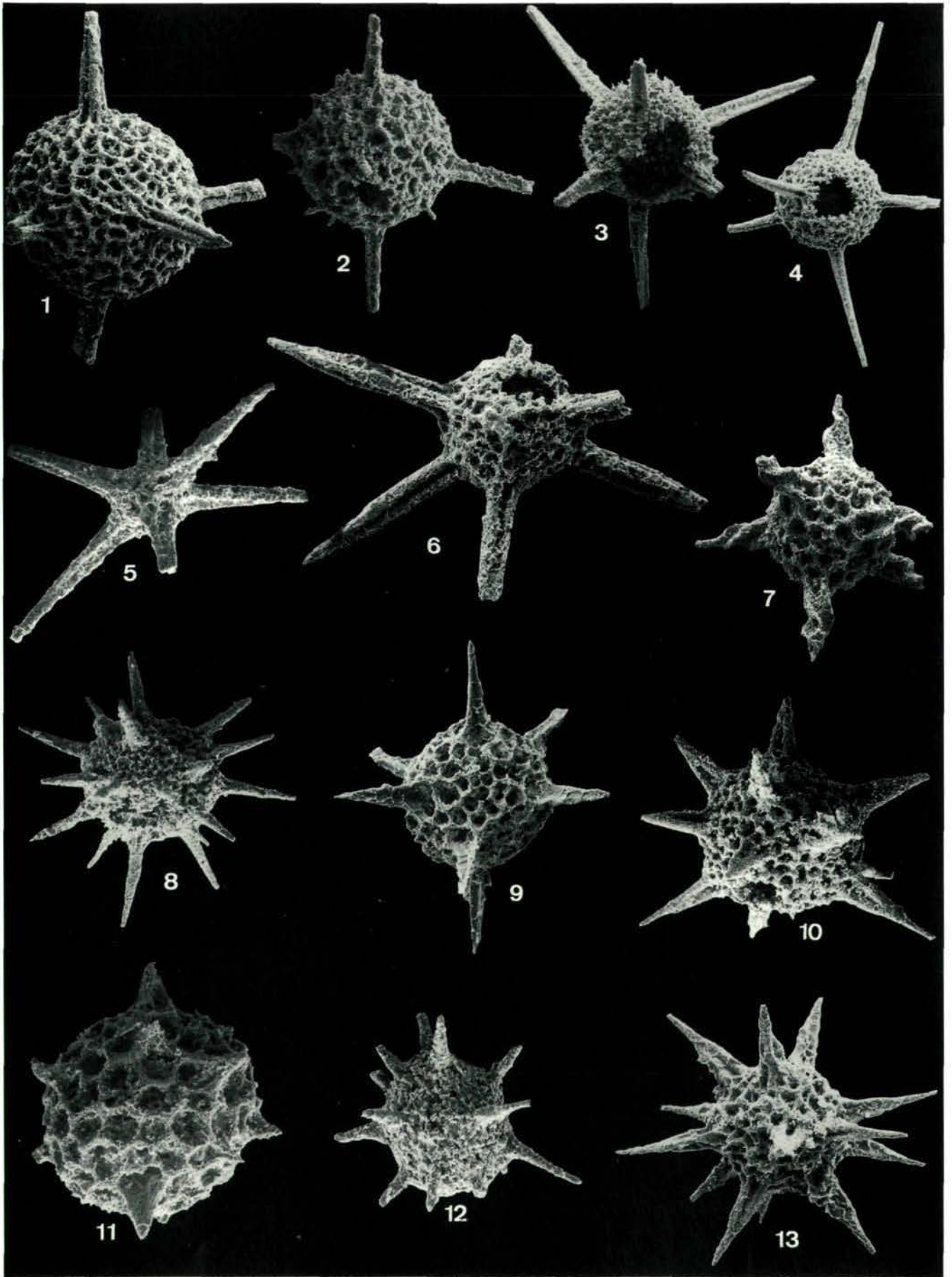
Plate 8

Plate 9

Figs. 1, 2:   *Pentactinocapsa multispinosa* n. sp., x 170, sample WW 7, rep.-no. KKM 1995/I-106, Fig. 1: lateral view, Fig. 2: oblique lateral-upper view.

Figs. 3, 4 ?, 5, 6, 7–9 ?, 10, 14:   *Pentactinorbis dumitricai* KOZUR & MOSTLER, 1994; Fig. 3. x 200, sample WW 3, rep.-no. KKM 1995/I-96; Fig. 4: x 200, sample WW 12, rep.-no. KKM 1995/I-97; Fig. 5: x 220, sample WW 12, rep.-no. KKM 1995/I-98; Fig. 6: x 200, sample WW 6, rep.-no. KKM 1995/I-99; Fig. 7: x 150, sample WW 7, rep.-no. KKM 1995/I-100, Fig. 8: x 160, sample WW 8, rep.-no. KKM 1995/I-101; Fig. 9: x 150, sample WW 12, rep.-no. KKM 1995/I-102; Fig. 10: x 160, sample WW 3, rep.-no. KKM 1995/I-103, Fig. 14: x 160, sample WW 8, rep.-no. KKM 1995/I-104.

Fig. 11:   *Pentactinocapsa awaensis* (NAKASEKO & NISHIMURA, 1979), x 160, sample WW 3, rep.-no. KKM 1995/I-105.

Figs. 12, 13:   *Cenosphaera parvispinosa* n. sp.; Fig. 12: x 200, sample WW 7, rep.-no. KKM 1995/I-107; Fig. 13, holo-type, x 180, sample WW 6, rep.-no. KKM 1995/I-2.

Figs. 15-18:   *Acanthosphaera carterae* n. sp.; Fig. 15: x 200, sample WW 12, rep.-no. KKM 1995/I-108; Fig. 16; holo-type, x 175, sample WW 9, rep.-no. KKM 1995/I-12; Fig. 17: x 200, sample WW 6, rep.-no. KKM 1995/I-109; Fig. 18: x 250, sample WW 3, rep.-no. KKM 1995/I-110.
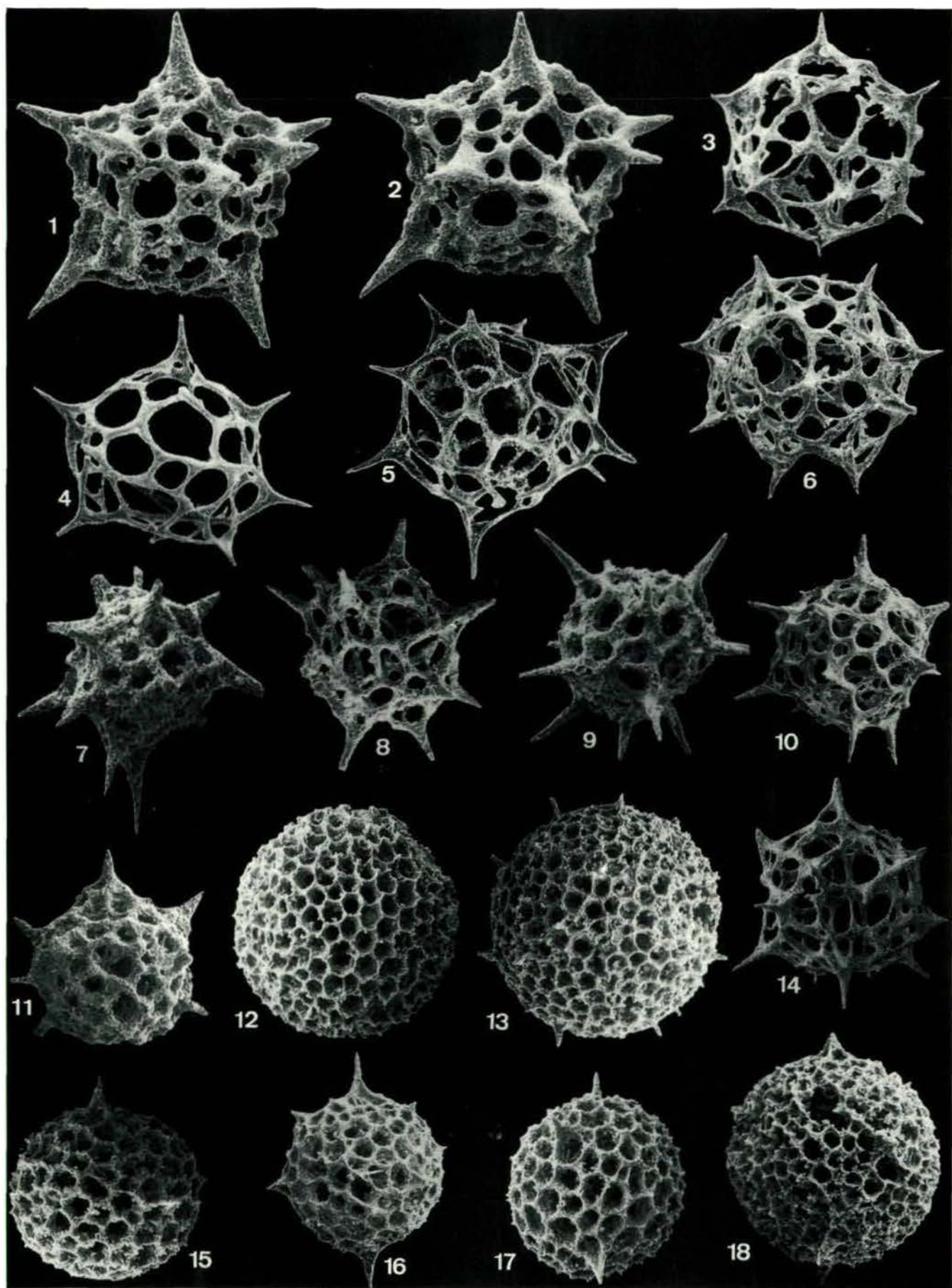
Plate 10

Figs. 1–4, 6, 10 ?: *Eptingium manfredi manfredi* DUMITRICĂ, 1978a; Fig. 1: x 200, sample WW 12, rep.-no. KKM 1995/I-111;
Fig. 2: x 170, sample WW 12, rep.-no. KKM 1995/I-112; Fig. 3: x 130, sample WW 13, rep.-no. KKM 1995/I-113; Fig. 4: x 200, sample WW 9, rep.-no. KKM 1995/I-114; Fig. 6: x 170, sample WW 8, rep.-no. KKM 1995/I-115; Fig. 10: x 200, sample WW 6, rep.-no. KKM 1995/I-116.

Fig. 5: *Eptingium* sp., x 140, sample WW 9, rep.-no. KKM 1995/I-117.

Fig. 7: *Eptingium manfredi japonicum* NAKASEKO & NISHIMURA, 1979, x 140, sample WW 3, rep.-no. KKM 1995/I-118.

Fig. 8: *Eptingium ramovsi* n. sp., x 200, sample WW 6, rep.-no. KKM 1995/I-119.

Figs. 9, 13, 14, 15 ?: *Triassistephanidium anisicum* n. sp., x 200; Fig. 9: holotype, sample WW 7, rep.-no. KKM 1995/I-3; Fig. 13: sample WW 12, rep.-no. KKM 1995/I-120; Fig. 14: sample WW 6, rep.-no. KKM 1995/I-121; Fig. 15: sample WW 9, rep.-no. KKM 1995/I-122.

Fig. 11: *Staurolonche praegranulosa* n. sp., holotype, x 100, sample WW 9, rep.-no. KKM 1995/I-14.

Fig. 12: *Cryptostephanidium cornigerum* DUMITRICĂ, 1978a, x 200, sample WW 12, rep.-no. KKM 1995/I-123.

Fig. 16: *Staurolonche trispinosum trilobum* (NAKASEKO & NISHIMURA, 1979), x 140, sample WW 4, rep.-no. KKM 1995/I-124.
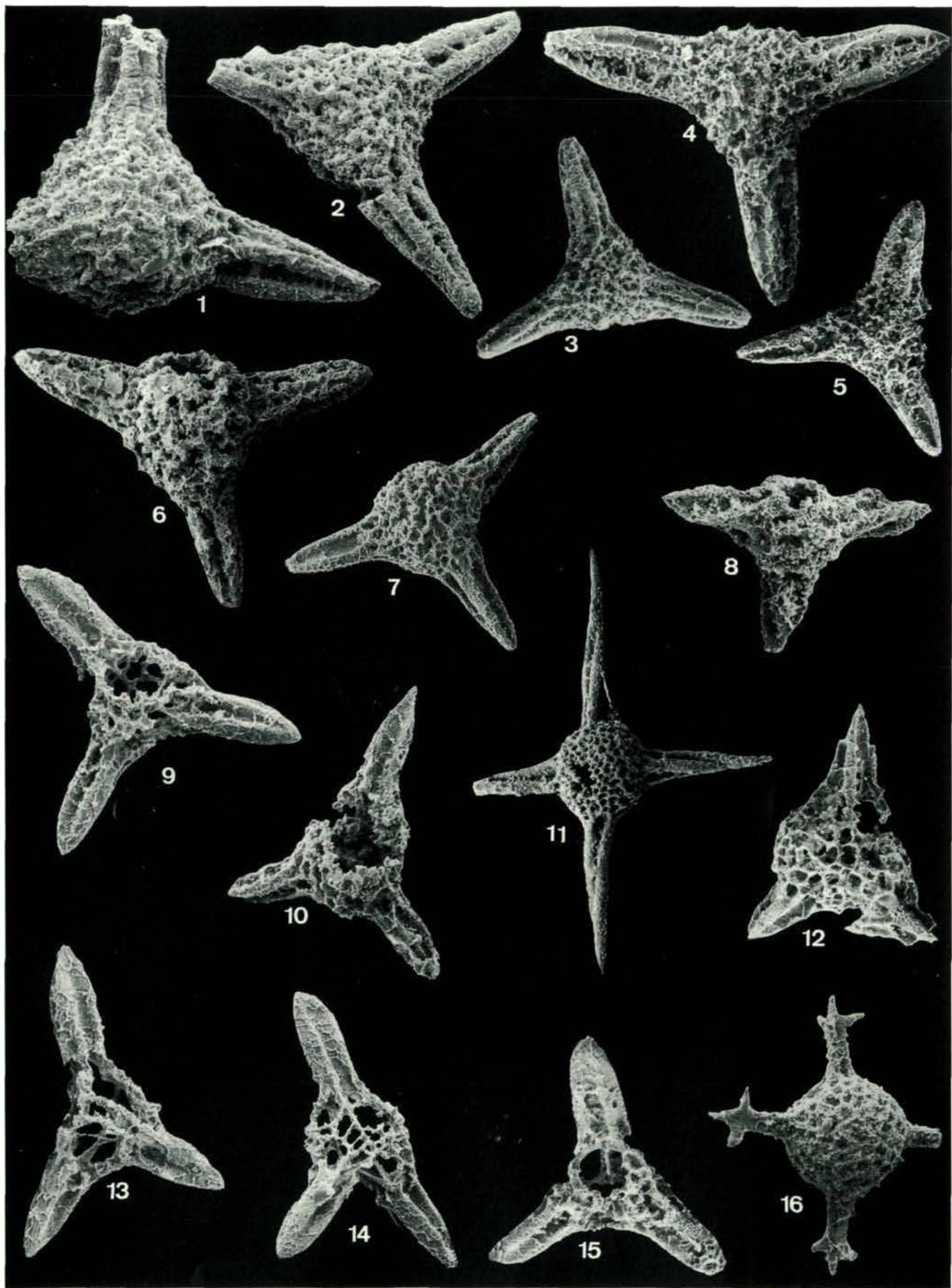
Plate 11

Figs. 1, 2, 4–7: *Tandarnia recoaroense* DUMITRICĂ, 1983; Fig. 1: x 280, sample WW 3, rep.-no. KKM 1995/I-125; Fig. 2: x 280, sample WW 4, rep.-no. KKM 1995/I-126; Fig. 4: x 200, sample WW 6, rep.-no. KKM 1995/I-127; Fig. 5: x 200, sample WW 7, rep.-no. KKM 1995/I-128; Fig: 6: x 220, sample WW 8, rep.-no. KKM 1995/I-129; Fig. 7: x 250, sample WW 12, rep.-no. KKM 1995/I-130.

Fig. 3: *Triassothamnus verticillatus* (DUMITRICĂ, 1978b), x 170, sample WW 9, rep.-no. KKM 1995/I-131.

Fig. 8: *Parentactinia pugnax* DUMITRICĂ, 1978b, x 500, sample WW 7, rep.-no. 15-8-95/I-16.

Fig. 9: *Poulpus illyricus* KOZUR & MOSTLER, 1994, x 500, sample WW 7, rep.-no. 15-8-95/I-15.

Fig. 10: *Paurinella fusina* (FENG, 1992), x 150, sample WW 8, rep.-no. 15-8-95/I-29.

Fig. 11: *Eptingium nakasekoi* KOZUR & MOSTLER, 1994, entactinarian spicular system well visible, x 200, sample WW 7, rep.-no. 15-8-95/I-14.

Fig. 12: *Paroertlispongus multispinosus* KOZUR & MOSTLER, 1981, isolated main spine, typical preservation for Oertlispongidae, x 200, rep.-no. 15-8-95/I-7.
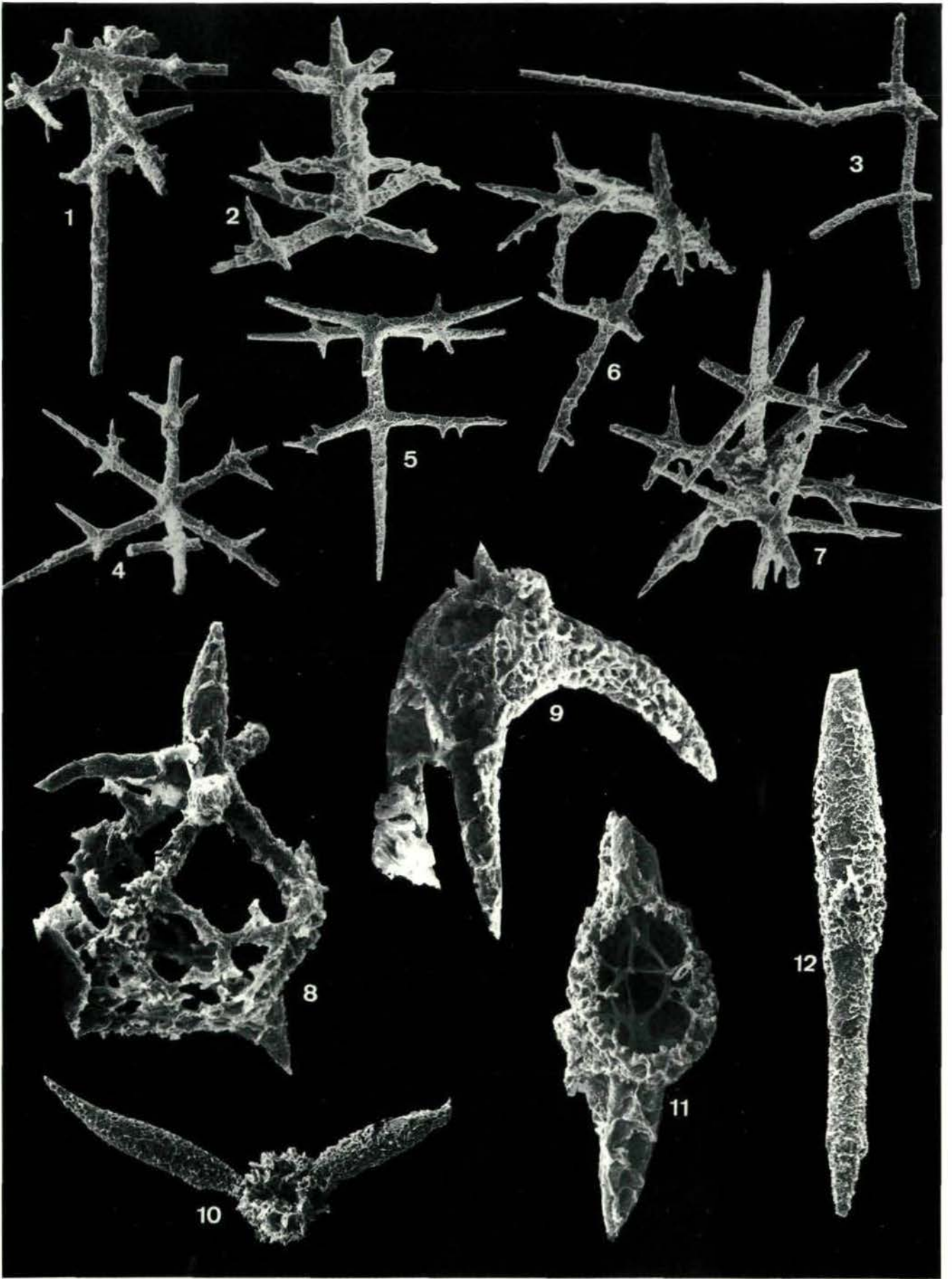
Plate 12

Facies and thin section photomicrographs showing microfacies types of the Loibl Formation (Figs. 1, 3–6: Selenischniak Member, Fig. 2: Weiße Wand Member). Scale bar 1 mm.

Fig. 1: Red nodular limestones exposed along the Selenitza forest road.

Fig. 2: Bioclastic wackestone rich in radiolarians and filaments, with pelmicritic matrix and some calcite cement. Weiße Wand, sample RJ 2.

Fig. 3: Bioclastic wackestone containing abundant echinoderm and shell fragments, a few other bioclasts and a micritic matrix. Selenitza forest road, sample ZE 5.

Fig. 4: Bioclastic wackestone/packstone, abundant echinoderm fragments and some other bioclasts, micritic intraclasts and a few altered volcanic rock fragments. The matrix consists of micrite, locally of calcite cements. Selenitza forest road, sample ZE 3a.

Fig. 5: Bioclastic grainstone/packstone with abundant echinoderm and shell fragments, cemented by calcite spar. Selenitza forest road, sample ZE 4.

Fig. 6: Poorly sorted carbonate breccia (debris flow) composed of angular and subangular clasts. The clasts represent different types of carbonate rocks derived from shallow-water carbonates as well as from the Loibl Formation (containing radiolarians). Selenitza forest road, sample ZE 8.
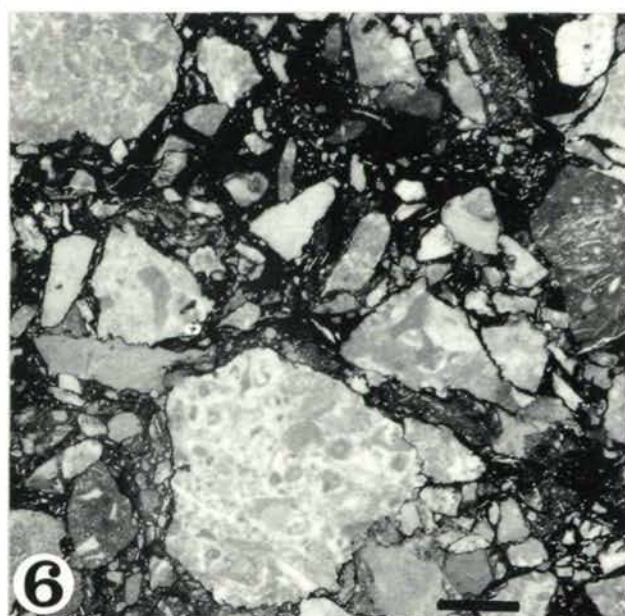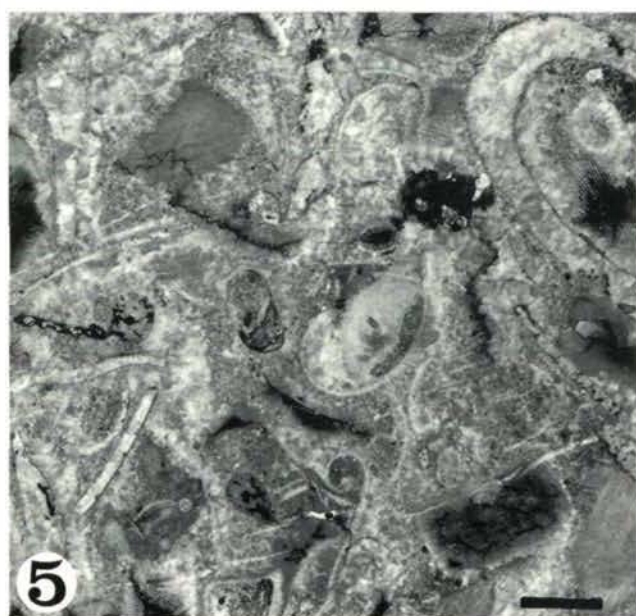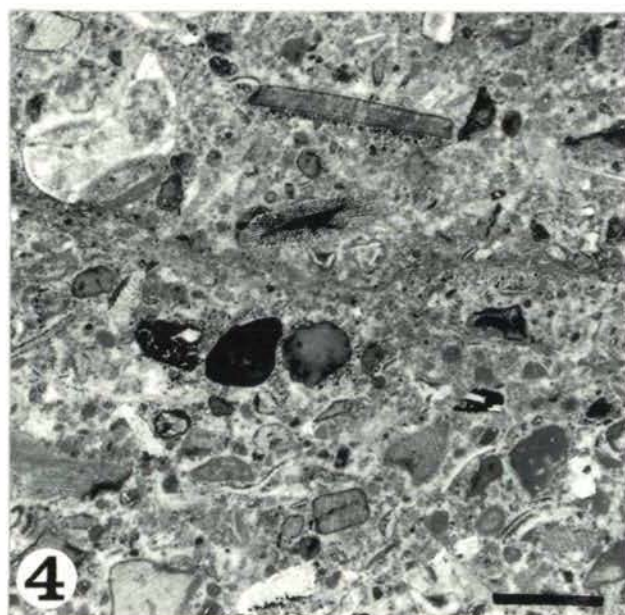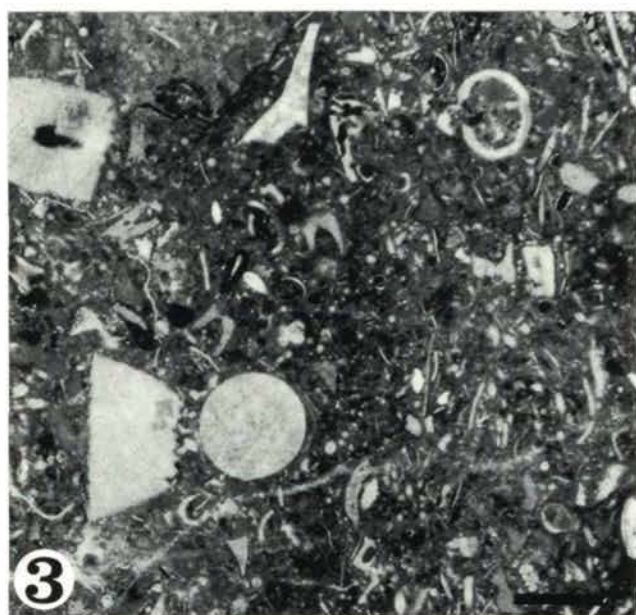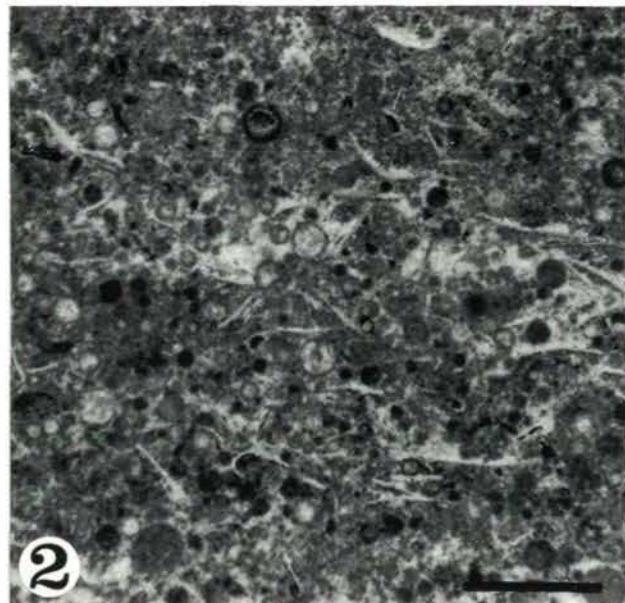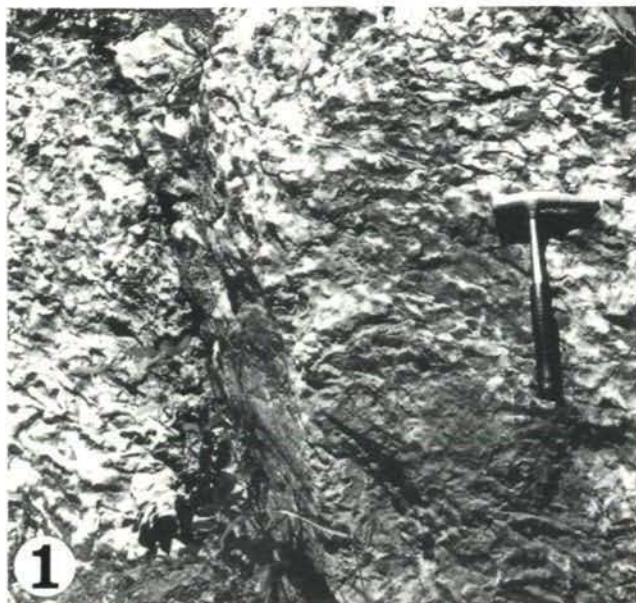
Plate 13

Thin section photomicrographs showing microfacies types of the Selenischniak Member of the Loibl Formation (Figs. 1–3, 5, 6) and of the Contrin Formation (Fig. 4). Scale bar = 1 mm.

Fig. 1: Filament packstone consisting of densely packed, thin shell fragments (filaments), some pelmicritic matrix and calcite spar. Selenischniak, sample LB 5.

Fig. 2: Bioclastic wackestone/packstone containing a large fragment of a hexactinellid sponge. Selenischniak, sample LB 11.

Fig. 3: Bioclastic wackestone containing a large fragment of a hexactinellid sponge. Selenischniak, sample LB 12.

Fig. 4: Algae-Tubiphytes bindstone from the uppermost Contrin Formation at the Zeller Prapotnik. Pore space is filled with calcite spar and subordinately with pelmicritic matrix. Zeller Prapotnik, sample PR 2.

Fig. 5: Bioclastic wackestone/packstone with abundant radiolarians and some shell fragments and other bioclasts. The matrix consists of micrite. Zeller Prapotnik, sample PR 5.

Fig. 6: Bioclastic wackestone containing abundant filaments and angular carbonate lithoclasts, mostly derived from shallow-water carbonates (Contrin Formation). Loibl Formation, Zeller Prapotnik, sample PR 15.
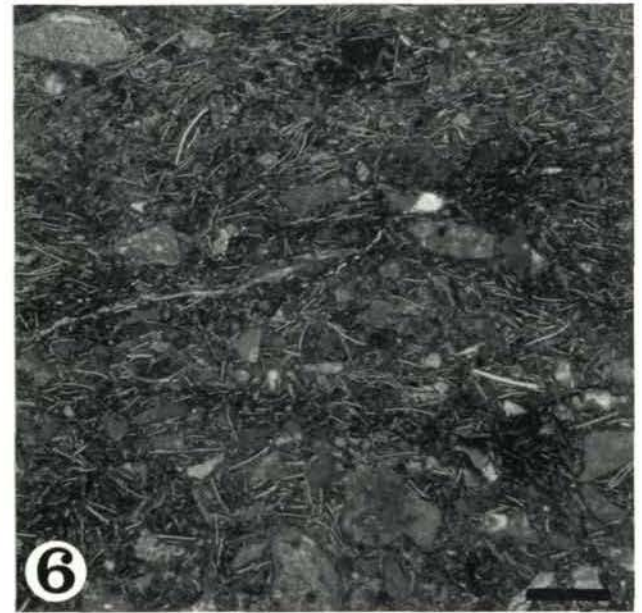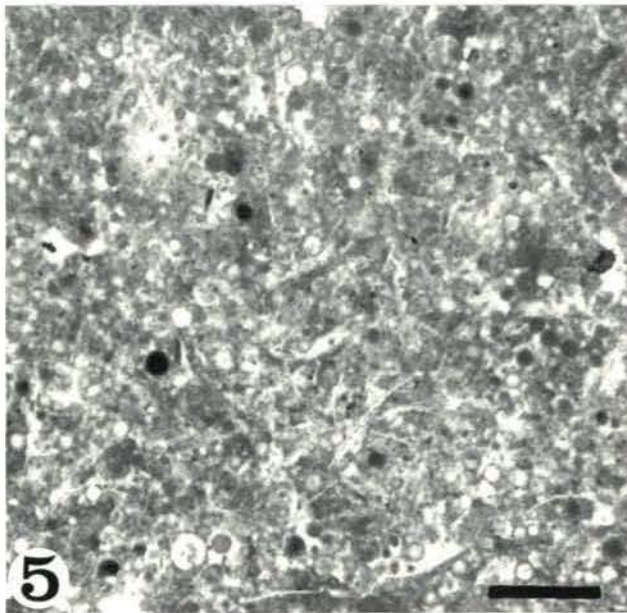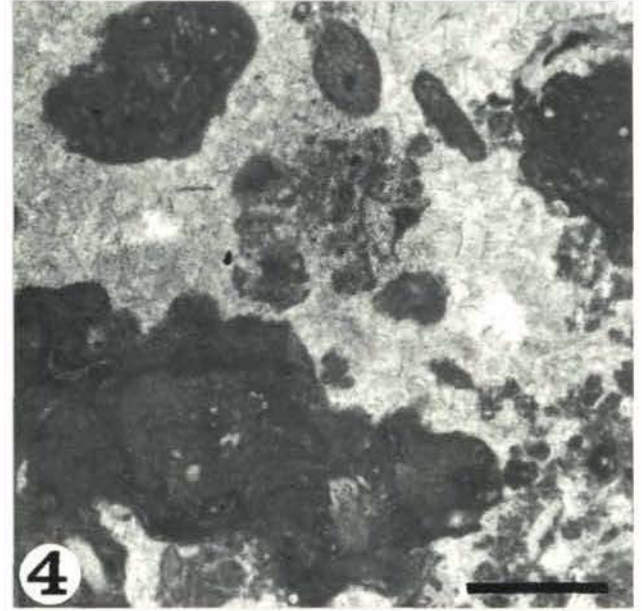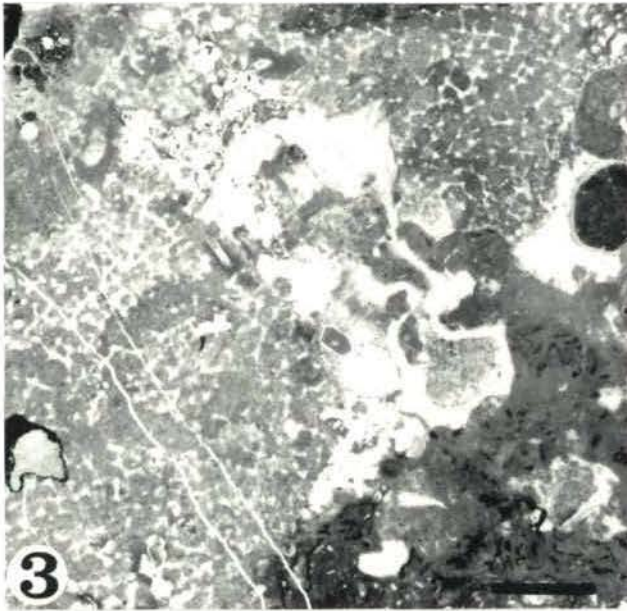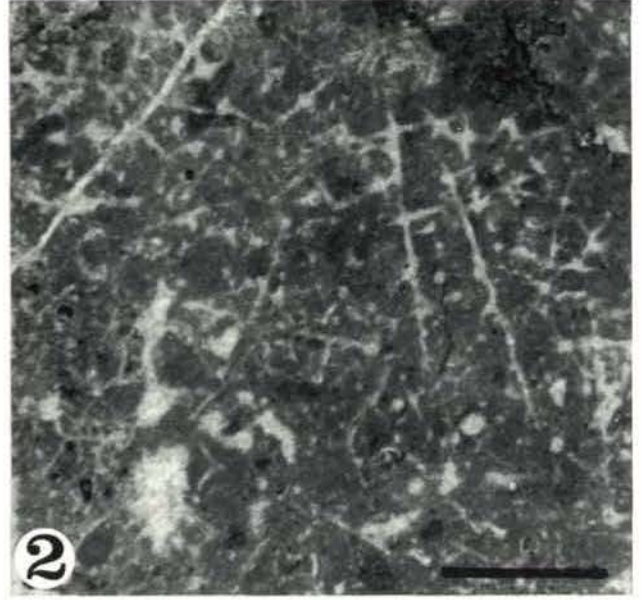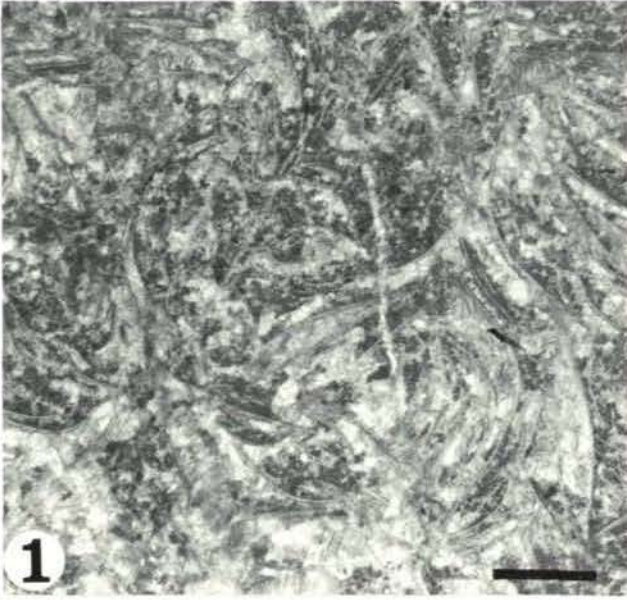
FIRST EVIDENCE OF LOWER TO MIDDLE SCYTHIAN (DIENERIAN – LOWER OLENEKIAN) RADIOLARIANS FROM THE KARAKAYA ZONE OF NORTHWESTERN TURKEY

Heinz W. Kozur, Orhan Kaya & Helfried Mostler

With 1 figure and 2 plates

Abstract:

Stigmosphaerostylus turkensis n. sp., a new entactinarian radiolarian species, is described from Dienerian to lower Smithian (Lower to lower Middle Scythian) limestones from the Karakaya Zone of northwestern Turkey. It is the oldest known Triassic radiolarian species. The nearly complete disappearance of Radiolaria at the Permian-Triassic boundary and the development of the Lower Triassic radiolarian faunas is discussed. Nassellaria have obviously evolved during the Spathian (Upper Scythian) from spicular Entactinaria without shell, but also many shell-bearing Triassic Entactinaria evolved during that time from spicular Entactinaria. The radiolarians and conodonts are accompanied by the oldest siliceous sponge spicule fauna of the Triassic. As the radiolarian fauna, only a very monotonous fauna with pentactine and very rare hexactine spicules (Hexactinellida, Lyssakida) is present that can be regarded as a pioneer fauna belonging probably only to one species.

Zusammenfassung:

Stigmosphaerostylus turkensis n. sp., eine neue Entactinaria-Radiolarienart aus dem Dienerian bis unteren Smithian (Unterskyth bis tieferes Mittelskyth) der Karakaya-Zone (nordwestliche Türkei) wird beschrieben. Das nahezu vollständige Aussterben der Radiolarien and der Perm-Trias-Grenze und die Entwicklung der untertriassischen Radiolarienfaunen wird diskutiert. Nassellaria haben sich offensichtlich erst während des Spathian (Oberskyth) aus spicularen Entactinaria ohne Schale entwickelt, aber auch viele Schalen-tragende triassische Entactinatinaria entwickelten sich in diesem Zeitraum aus spicularen Entactiniaria. Die Radiolarien und Conodonten werden von der ältesten bekannten triassischen Kieselschwammspiculae-Fauna begleitet. Wie die Radiolarienfauna sind auch die Schwammspiculae sehr monoton und bestehen im wesentlichen aus glatten Pentactinen und sehr wenigen glatten Hexactinen von Hexactinellida (Lyssakida). Sie repräsentieren eine Pionierfauna, die vielleicht nur aus einer Art besteht.

1. Introduction

Radiolarians are still very common in the Upper Changxingian, but nearly disappeared near the P/T boundary. In Sicily, a very rich Upper Changxingian radiolarian fauna occurs in red deep water clays with *Clarkina changxingensis* (WANG & WANG), *C. sosioensis* GULLO & KOZUR and *Hindeodus latidentatus* KOZUR, MOSTLER & RAHIMI-YAZD (KOZUR, 1993, 1995 a, b). Red deep water clays of that age contain up to several 10 000 radiolarians per kg̃ clay. Pelagic Lower Scythian (Brahmanian) beds of Sicily did not yield radiolarians; also calci-

fied radiolarians are absent in pelagic Lower Scythian limestones. Radiolarians re-appear in this area only in the upper Scythian (Upper Olenekian, Spathian)

Rich radiolarian faunas occur also in the uppermost Changxingian of southwest China (FENG, QINGLAI, 1992, FENG, QINGLAI & LIU, BENPEI, 1993 a). In the Shangsi section, one of the present authors (KOZUR) found rich radiolarian faunas in Upper Changxingian siliceous limestones immediately below the Transitional Beds. In the Transitional Beds suddenly the radiolarians disappeared and, as in the Lower Scythian (Brahmanian), even

siliceous rocks are absent;·also thin sections of Lower Scythian pelagic limestones did not show any radiolarian remains. Assumed Lower Scythian radiolarites of southwest China are of Middle Triassic age (see chapter 4.).

In Japan and SE Siberia the stratigraphic control of the youngest Permian faunas is not so good as in China and Sicily. However, the *Neoalbaillella ornithoformis* Zone can be well dated in China as Lower Changxingian (FENG, QINGLAI & LIU, BENPEI, 1993 b). For this reasons, the *Neoalbaillella grypus* Zone of Japan (KOZUR & MOSTLER, 1989; for range chart of the species, see ISHIGA, 1990) probably corresponds to the Upper Changxingian. Both in Japan and in SE Siberia, the Changxingian radiolarites are overlain by black anoxic shales. The boundary between the hard radiolarites and the soft black shales is always strongly tectonized, but the entire Lower Scythian is free of radiolarians and even siliceous intercalations are missing. Only a few spherical microradiolarians (shells with about 40 µm diameter) were found in these beds.

The youngest Permian radiolarian faunas from the Grindstone terrane in Oregon (USA) may also belong to the Upper Changxingian, because *Neoalbaillella grypus* ISHIGA, KITO & IMOTO was reported (BLOME & REED, 1992).

The oldest Triassic radiolarians and shale-radiolarite sequences are known from the Upper Scythian (Upper Olenekian, Spathian) of the Circum-Pacific realm, especially from Japan and SE Siberia (SASHIDA, 1983, 1991, BRAGIN, 1991 SUGIYAMA, 1992, NAGAI & MITZUANI, 1993). Only in the Grindstone terrane, Smithian (Lower Olenekian) radiolarians were found in limestones, but not yet described (BLOME & REED, 1992). The only Scythian radiolarians outside the Circum-Pacific realm have been found in the Monte Facito Formation of the Lagonegro Basin in southern Italy (MARSELLA et al., 1993). There, the radiolarian-bearing limestones occur in the uppermost Spathian *Chiosella gondolelloides* Zone. Radiolarians are common also in Spathian pelagic micritic limestones of the Sosio Valley (Sicily, Italy), but all are calcified and cannot by dissolved from these limestones.

In western Turkey, two areas were investigated for Scythian radiolarians. In the Karaburun peninsula well dated Spathian to Ladinian red and gray pelagic limestones (partly with intraformational breccia or conglomeratic), red shales, in the Anisian and Ladinian additionally reddish and greenish radiolarites and intermediate volcanics are present. The red radiolarites yielded rich Lower Anisian to Ladinian radiolarian faunas. As in other areas, the Lower Anisian radiolarians are not much diversified, but Entactinaria, Spumellaria and Nassellaria are present. Scythian radiolarians were not found. According to ERDOĞAN et al. (1990, 1995) this well dated sequence (their Gerence Formation) interfingers with a "Scythian-Anisian" clastic sequence (Karaeis Formation sensu ERDOĞAN et al., 1990, 1995) that is rich in black and greenish gray radiolarites. These radiolarites were investigated for radiolarians and other microfossils, but they yielded only Silurian to Lower Carboniferous radiolarians, conodonts and Muellerisphaerida (KOZUR, in press). No evidence for a sedimentological interfingering between these Paleozoic radiolarites and the well dated Spathian to Ladinian rocks of the Gerence Formation can be found.

The second studied area for Scythian radiolarians is situated in the Karakaya Zone. WIEDMANN et al. (1992) proved there the presence of a pelagic, partly oceanic Scythian and Middle Triassic rocks and KOZUR & KAYA (1994) found latest Permian pelagic conodonts. In this area the search for Scythian conodonts was successful and in limestones the oldest Scythian radiolarians and siliceous sponge spicule associations of Dienerian to Smithian (Late Brahmanian to Early Olenekian) age were discovered that are well dated by conodonts.

2. Locality data and geological setting

The investigated area lies in northwestern Turkey, NE of Bursa (Fig. 1 A). It belongs to the Karakaya Zone that is interpreted in different manner. According to ŞENGÖR et al. (1980), ŞENGÖR (1984, 1985) it is the main suture zone of the Paleozoic to
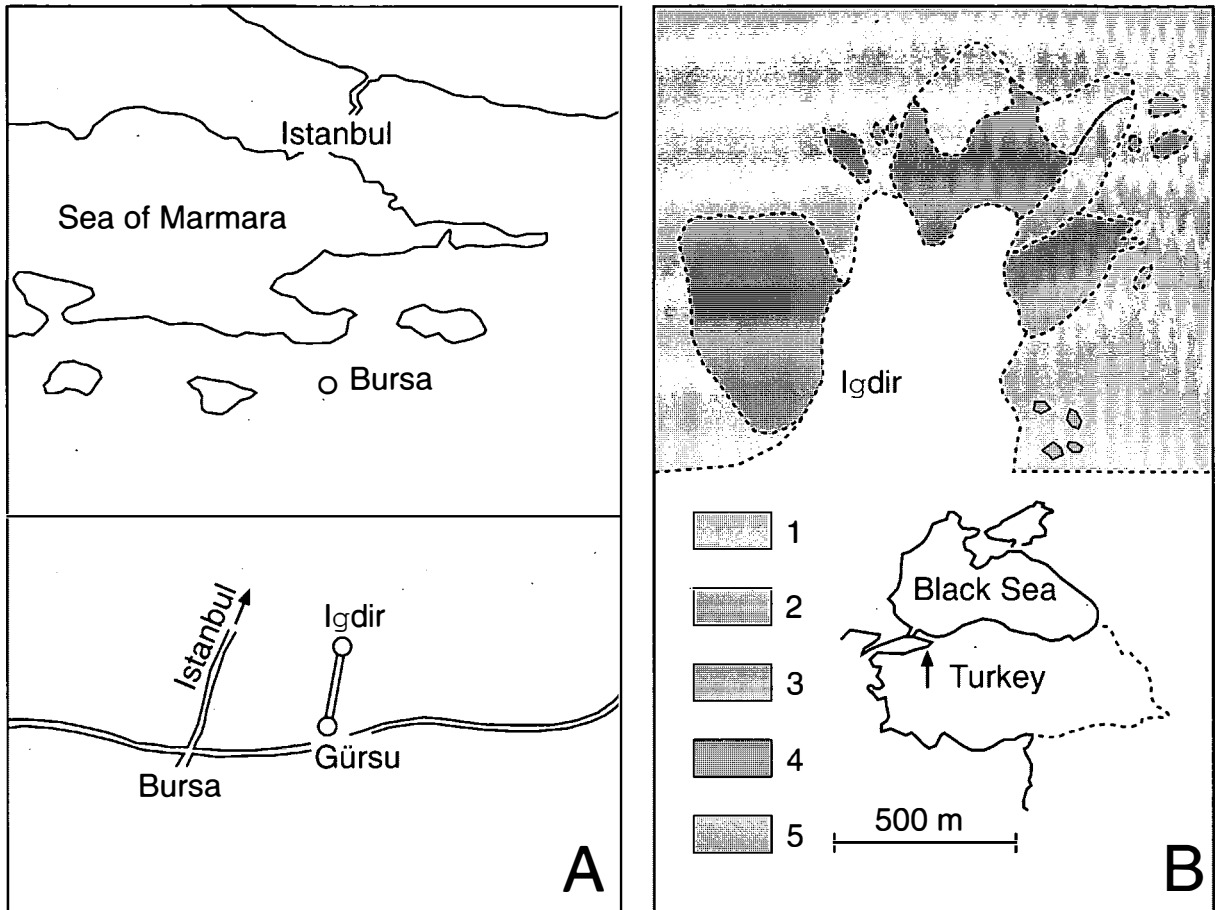
Fig. 1: Location map.

A: Geographic location of Igdir, NE of Bursa, northwestern Turkey.

B: Geological situation in the locality with Scythian radiolarians: 1 = Upper Triassic turbidite-olistostrome unit (turbiditic sandstones and shales; supporting matrix for the older blocks). 2 = Block of *Halobia* bearing Lower Norian limey lithic sandstones and shales, contemporaneous with parts of the turbidite-olistostrome unit. 3 = Scythian block of pelagic shales, thinly bedded, dark, marly limestones, lithic sandstones and minor fine-grained lithic conglomerates. the limestones contain conodonts, radiolarians and sponge spicules. 4 = Blocks of pelagic Upper Scythian and Middle Triassic limestones, partly Hallstatt Limestones with ammonoids. 5 = Blocks of limey lithic sandstones, age undated.

Middle Jurassic Paleotethys. The Upper Triassic turbidite-olistostrome unit was interpreted as a subduction-related unit indicating the closing of the Karakaya branch of the Paleotethys during the end of the Triassic.

KOZUR (1991 a, b, and in press) regarded also the Karakaya Zone as a suture zone and the Upper Triassic turbidite-olistostrome unit with blocks of ultrabasites, basic volcanics, radiolarites and Middle Triassic to Cordevolian metamorphics as subduction related accretionary complex of an oceanic sequence that contains also blocks of pelagic slope limestones as well as extrabasinal limestones. Middle Triassic metamorphic rocks (KAYA & MOSTLER, 1992) and Lower Carnian metamorphic rocks (KAYA & KOZUR, in prep.) were regarded as subduction related metamorphics. The closing of the Karakaya oceanic branch was assumed at the end of the Triassic. However, according to KOZUR (1991 a, b, and in press), the Karakaya oceanic branch was not part of a Paleozoic-Triassic Paleotethys, but part of the southern branch of Cimmerian Ocean that opened in western Turkey in the uppermost Permian, had the fastest sea-floor spreading in the Middle Triassic and closed in the Karakaya branch during the

Upper Triassic, in the northern branch during the Upper Jurassic. Blocks of pelagic Paleozoic beds within the Upper Triassic turbidite-olistostrome unit of the Karakaya Zone have a Silurian to Early Carboniferous age. No Middle and Upper Carboniferous and Lower Permian rocks are known, Middle Permian olistoliths are extrabasinal shallow water carbonates (fusulinid limestones). The breaking up of this carbonate platform is indicated by uppermost Dzhulfian and Changxingian pelagic limestones (KOZUR & KAYA, 1994). Toward the margin of the Istanbul block (that separated the Karakaya Zone from the northern branch of the Cimmerian Ocean), the entire Permian was missing and the Lower Triassic began with an onlap sequence to which belong also the investigated Scythian rocks with radiolarians.

In this connection, some remarks to the paper OKAY & MOSTLER (1994) are necessary. Despite the fact that H. MOSTLER is listed as co-author, he has neither got the manuscript nor the printed paper. We have learned about the existence of this paper from a paper of STAMPFLI (1966), but were not yet able to get this paper. From the title of the paper and the paper of STAMPFLI (1996) we know that in this paper the existence of Carboniferous and Permian radiolarite blocks in the Karakaya Zone was indicated. Two of the co-authors (KOZUR & MOSTLER) have seen the material (pelagic limestones and radiolarites) of OKAY (sent by L. KRYSTYN, Vienna) and together determined the age. In a part of the material Lower Carboniferous conodonts and indeterminable radiolarians are present that belong to unspecific, poorly preserved Entactinaria with genera that could occur in the long time span at least from the Devonian to Lower Triassic. Because of the presence of Lower Carboniferous conodonts they are of Mississippian age. In some radiolarites only these radiolarians were present. From the fact that the radiolarian faunas of the conodont-bearing rocks (Lower Carboniferous) and conodont free radiolarites (probably also Lower Carboniferous, but with indeterminable radiolarians) consist of Entactinarian genera that have a long range from the Devonian to the Lower or Middle Triassic, OKAY seemingly concluded that they are (Devonian) early Carboni-

ferous to Permian in age which is not the case. Permian radiolarites contain always (beside the mentioned long-ranging Entactinaria genera) specific Permian radiolarians (mostly advanced Albaillellacea, Ruzhencevicea, advanced Entactinaria), well known to the present authors. Such radiolarians were not present in the material of OKAY, and this excludes the presence of Permian radiolarites in his material. Because this manuscript was not sent to the co-author, MOSTLER, this serious mistake was not corrected and lead by STAMPFLI (1996) to the incorrect correlation of the Karakaya Zone of northwestern Turkey (with assumed, but really not present Lower Permian radiolarites) and the Sicanian Zone of western Sicily with Lower Permian deep sea sediments (even with deep-sea trace fossils, KOZUR, KRAINER & Mostler, 1996). In the Lower Permian, the Karakaya Zone was a subaerial denudation area without sediments and nowhere in western Turkey Lower Permian deepwater sediments are known. Few areas (Ankara-Izmir Zone) have yielded shallow-water fusulinid limestones from the upper part of the Lower Permian.

According to KAYA (1992) the entire area of western Turkey was regionally metamorphosed during the Middle Triassic and the Upper Triassic turbidite-olistostrome unit is an onlap sequence.

The investigated area lies at the northern margin of the Karakaya Zone at the margin of the Istanbul block. Like on the Istanbul block, the Middle Carboniferous to Permian interval is missing and the Triassic is transgressive. The oldest block in the Upper Triassic turbidite-olistostrome unit is a Lower Triassic block (Fig. 1 B) that begins with sandstones, siltstones, shales and conglomerates overlain by shales and thin dark, marly and silty sandstone. It is a typical transgressive onlap series different from the central Karakaya Zone, where Middle and Upper Permian shallow water limestones are followed by Upper Dzhulfian and Changxingian (uppermost Permian) pelagic limestones and Lower Triassic pelagic limestones that are intercalated with basic volcanics during the Upper Scythian (Spathian = Upper Olenekian).

Middle Triassic blocks that are adjacent to the lower Triassic block of the investigated area con-

sists of ammonoid-bearing Hallstatt Limestones and other pelagic limestones, whereas blocks of Middle Triassic radiolarites, pillow lavas and ultrabasites are missing in that area. Consequently, the investigated area belong to the northern slope of the Karakaya Basin or at least the blocks within the Upper Triassic turbidite-olistostrome sequence have been derived exclusively from the northern slope of the Karakaya Basin adjacent to the Istanbul Block.

The radiolarian-bearing Scythian limestones are dark gray to black, marly to silty limestones. They are well dated by conodonts. Sample K 7324 contains *Neospathodus dieneri* SWEET (Pl. 2, Figs. 11, 12) and *Clarkina procerocarinata* KOZUR (Pl. 2, Fig. 10) and can be dated as lower Dienerian (Brahmanian). Sample K 7323 (with the richest radiolarian fauna) yielded *N. dieneri* and *N. conservativus* (MÜLLER) (Pl. 2, Fig. 9), and can be dated as Dienerian to lower Smithian (uppermost Brahmanian to lowermost Olenekian). The present, mostly poorly preserved radiolarians are the oldest known Triassic radiolarians of the world. Their diversity is very low, but also all other faunas have a low diversity as typical for the Lower Scythian faunas. Beside radiolarians there are pelagic conodonts, ostracods (Pl. 1, Fig. 9) and siliceous sponge spicules.

3. Systematic descriptions

Subclass Radiolaria MÜLLER, 1858
Order Polycystida EHRENBERG, 1838
Suborder Entactinaria
KOZUR & MOSTLER, 1982
Superfamily Hexastylacea HAECKEL, 1882
emend. PETRUSHEVSKAYA, 1979

Family Triposphaeridae
VINASSA DE REGNY 1898,
emend. Kozur & Mostler, 1981

Synonyma:
Dorysphaeridae VINASSA DE REGNY, 1898
Entactiniidae RIEDEL, 1967

Genus *Stigmosphaerostylus* RÜST, 1892

Type species: *Stigmosphaerostylus notabilis* RÜST, 1892
Synonyma:
Ellipsostigma HINDE, 1899
Centrolonche POPOFSKY, 1912
Entactinia FOREMAN, 1963

Stigmosphaerostylus turkensis n. sp.
(Pl. 1, Figs. 1–6)

Derivatio nominis: According to the occurrence in Turkey.
Holotypus: The specimen on Pl. 1, Fig. 1; rep.-no. 4-8-95/I-11
Locus typicus: Scythian block 500 NE of Igdir (NE of Bursa, northwestern Turkey).
Stratum typicum: Thin-bedded black marly limestone within dark shales and siltstones, upper Dienerian or lower Smithian; sample K 7323.
Material: More than 100, mostly badly preserved specimens.
Diagnosis: The shell is coarsely latticed and has triangular to hexagonal pores. The 7 three-bladed main spines are as long as the shell diameter or somewhat shorter to somewhat longer. The vertices of the pore frames have needle-like by-spines. The internal spicular system is very robust, point-centred and consists of 7 tricarinate spines that are connected with the main spines.
Description: The single spherical, coarsely latticed shell has pores of irregular size and shape. Most of the pores are very large, but some are small. The outline of the pores differs from triangular to pentagonal, partly also hexagonal. All different pore outlines occur in one specimen. The main spines are tricarinate, long, slender, nearly of the same width throughout their length. The furrows between their three blades are deep and narrow. The length of the main spines varies. They are somewhat shorter to somewhat longer as the shell diameter. The vertices of the pore frames bear needle-like spinules of different length. The internal spicular system is very robust, point-centred and somewhat eccentric. It consists of 7 spines

that are connected with the 7 main spines. The spines of the spicular system are tricarinate (except their needle-like innermost parts) and become distinctly wider toward the base of the main spines.

Measurements:

Diameter of shell. 200-280 µm

Length of the main spines: 150-320 µm

Length of the by-spines: 28-60 µm

Occurrence: Dienerian and lower Smithian of the type locality.

Remarks: *Stigmosphaerostylus turkensis* n.sp. has a robust spicular system that is rather typical or Paleozoic Hexastylacea, whereas Mesozoic and Cenozoic Hexastylacea have in general a fragile, needle-like internal spicular system.

Most similar is *Stigmosphaerostylus nikorni* (SASHIDA & IGO, 1992) from the basal Anisian *Chiosella timorensis* Zone of Thailand. In this species the internal spicular system is more fragile (needle-like throughout their length, not distinctly broader near the base of the main spines). Moreover, the spicule is six-rayed. The 6–8 main spines taper gradually in distal direction.

Stigmosphaerostylus recticulata (SASHIDA & TONISHI, 1985) from the Upper Permian of Japan has similar pore frames, but the shell is smaller, the spicular system is bar-centred and displays only 6 rays that are connected to 6 main spines.

Suborder Spumellaria EHRENBERG, 1875
Superfamily Sponguracea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1981

Family, genus and spec. inc.
(Pl. 1; Figs. 7,8)

Remarks: Several spherical and ellipsoidal spongy radiolarians occur that have no external spines. Their shell consists of a thick spongy meshwork that fills nearly the entire test. The spherical and ellipsoidal forms belong probably to two different taxa. *Cenosphaera* sp. aff. *andoi* SUGIYAMA from the Spathian of Japan (NAGAI & MIZUTANI, 1993) may be identical with the spherical forms.

Arrangement in spongy shells cannot be observed in the present material (? because of the bad preservation) and consequently an assignment to the Oertlispongidae KOZUR & MOSTLER, 1980 (in DUMITRICĂ et al., 1980) is not possible. But they may be the ancestral forms of both the Oertlispongidae and Archaeospongoprunidae that begin both in the Lower Anisian.

Phylum Porifera GRANT, 1836
Class Hexactinellida SCHMIDT, 1870
Order Lyssakida ZITTEL, 1877

Pentactine spicules
(Pl. 2, Figs. 1–7)

Description: Smooth pentactine spicule. The four cross-like arranged paratangential rays (arranged in one plane) differs in their length. The proximal ray (rhabd) is broader and longer. It is situated perpendicular to the paratangential rays. Sometimes the paratangential rays are curved in direction to the rhabd (Pl. 2, Fig. 7). All spines become slowly, but continuously narrower from their common base to their distal ends.

Hexactine spicules
(Pl. 2, Fig. 8)

Remarks: Except the very short sixth spine opposite to the rhabd, this very rare spicule is very similar to the common pentactine spicule.

4. Discussion

Radiolaria were very strongly affected by the Permian-Triassic biotic crisis. Whereas radiolarians are still common and divers in the uppermost Changxingian, they are nearly missing in the Lower Scythian. Even in the Panthalassa Ocean, the organic silica production was interrupted during the Lower and Middle Scythian. The only reported exception from the absolute minimum in radiolarian diversity and the absence of cherts is southwest Yunnan of southwest China (FENG,

QINGLAI, 1992, FENG, QUINGLAI & LIU, BENPEI, 1993 a). According to these authors, the Muyinhe Formation of latest Permian to Middle Triassic age consists of radiolarites that are also uninterrupted present at the Permian-Triassic boundary and in the lower Scythian. Between the Upper Changxingian radiolarian fauna of sample My 30 and the assumed earliest Scythian sample My 27 are less than 20 cm of bedded cherts and shales. However, the *"Shengia yini* assemblage" of assumed lowermost Scythian is a typical Middle Triassic assemble. *Shengia yini* (FENG) is a specifically indeterminable totally recystallized *Triassocampe. Triassocampe soror* FENG & LIU that is rarely present in the *"Shengia yini* assemblage" and *Shengia nanpanensis* FENG & LIU that was reported from the upper part of the *"Shengia yini* assemblage", are both junior synonyma of *Triassocampe scalaris* DUMITRICĂ, KOZUR & MOSTLER. This species begins in the upper subzone of the uppermost Anisian *Spongosilicarmiger transitus* Zone (*Yeharaia annulata* Subzone). *Shengia solida* FENG that occurs in the *"Shengia yini* assemblage" and in the overlying assemblage, is a junior synonym of *Triassocampe deweveri* (NAKASEKO & NISHIMURA), a typical *Triassocampe* of the *S. transita* Zone that occurs also in the next younger zone, but not yet in the underlying *Tetraspinocyrtis laevis* Zone. *Yangia* sp. B from the lower *"Shengia yini* assemblage" is a *Paroertlispongus raridentatus* KOZUR & MOSTLER that also begins in the basal part of the *S. transitus* Zone and continues in the overlying *S. italicus* Zone. *Palaeoeucyrtis elongata* FENG comprises isolated main spines of *Paroertlispongus multispinosus* KOZUR & MOSTLER that typically becomes somewhat broader in distal direction. This species occurs in the uppermost Anisian *S. transita* Zone and in the Lower Ladinian. The isolated occurrence of the main spines of *Oertlispongus* and *Paroertlispongus* is a very typical preservation of oertlispongids. The more tumid isolated spines that were described as *Palaeoeucyrtis fusina* FENG are isolated spines of intermediellids (also a frequent preservation of different Intermediellidae taxa). A part of these spines can be assigned to *Paurinella* because *P. fusina* with corroded, but still present shell was

found in the *Tiborella florida* Subzone of the *Spongosilicarmiger transitus* Zone of late Illyrian age. The oldest *Paroertlispongus* (*P. diacanthus* SUGIYAMA, 1992) is known from the Lower Anisian of Karaburun peninsula (Turkey), but species in which the main polar spine that becomes broader in distal direction (*P. multispinosus*) appeared only in the upper Illyrian *S. transitus* Zone. Also *Paurinella* with *P. fusina* (FENG) and the perhaps partly identical *P. sinensis* (FENG) begins in the *S. transitus* Zone. *Praeyeharaia japonica* (NAKASEKO & NISHIMURA) from the lower „*Shengia yini* assemblage" occurs in the latest Anisian *S. transita* Zone and in the Lower Ladinian. A similar range has *Paroertlispongus chinensis* (FENG) that occurs in the upper *"Shengia yini* assemblage" and in the next younger assemblage of southwest Yunnan. In the European Tethys it occurs in the *S. transitus* Zone and in the lower part of the *Spongosilicarmiger italicus* Zone. Consequently, all determinable species of the *"Shengia yini* assemblage" occur in well dated radiolarian associations in the uppermost Anisian *S. transita* Zone and in the Lower Ladinian *S. italicus* Zone; partly they range to the middle Fassanian. *Paurinella fusina* seems to be restricted to the *S. transitus* Zone and therefore a latest Anisian age can be assumed for the *"Shengia yini* assemblage".

An assignment of the *"Shengia yini* assemblage" to the *S. transitus* Zone and not to the Lower Ladinian *S. italicus* Zone is confirmed by the age of the overlying *"Pseudoeucyrtis liui* assemblage" that belongs definitely to the upper *S. transita* Zone. *Pseudoeucyrtis liui* FENG is a junior synonym of *Archaeospongoprunum mesotriassicum* KOZUR & MOSTLER that has its uppermost range in the *S. transita* Zone, as *Tiborella anisica* (determined as *Cecrops floridus* NAKASEKO & NISHIMURA). *Paurinella sinensis* (FENG) is so far only known from the *S. transita* Zone and several species of the „*Pseudoeucyrtis liui* assemblage" have their first appearance in the *S. transita* Zone, as *Triassocampe deweveri*, *T. scalaris*, *Paroertlispongus hermi* (junior synonyma are discussed under *"Shengia yini* assemblage") and *Eptingium manfredi manfredi* DUMITRICĂ, all present in the „*Pseudoeucyrtis liui* assemblage". This is a typi-

cal association of the uppermost Anisian upper *S. transita* Zone (see KOZUR, 1995 c). The *"Pseudoeucyrtis liui* assemblage" was assigned by FENG, QINGLAI (1992) and FENG, QINGLAI & LIU, BENPEI (1993 a) to the late Early Triassic.

As pointed out above, both the assumed lowermost Scythian *"Shengia yini* assemblage"" and the assumed Upper Scythian *"Pseudoeucyrtis liui* assemblage" belong to the uppermost Anisian *S. transitus* Zone sensu Kozur (1995 c). Consequently, upper Changxingian radiolarites are immediately overlain by Upper Anisian radiolarites in the Muyinhe Formation. An other possibility is that the entire Muyinhe Formation is Middle Triassic and the uppermost Changxingian radiolarian fauna at the base of this formation is reworked. In any case, the so-called "early Early Triassic" *Shengia yini* assemblage is in reality a typical uppermost Anisian fauna. As clearly recognizable in the Shangsi section, also in southwest China the rich uppermost Changxingian radiolarian faunas disappear suddenly at the base of the Transitional Beds somewhat below the P/T boundary and the Lower Scythian sediments have not yielded any radiolarians and radiolarites.

The first Dienerian and lower Smithian Radiolaria that were found in Turkey fits well in this picture of a strong crisis in the radiolarian evolution at the P/T boundary and of a very slowly recovery of the radiolarian fauna after this crisis. Only primitive Entactinaria and Spumellaria are present and no more than 3 taxa were found. Only one species, the entactinarian *Stigmosphaerostylus turkensis*, is common.

All characteristic Upper Paleozoic radiolarians except Entactinaria and primitive Spumellaria disappeared at the P/T boundary. The presence of Albaillellacea in the Upper Scythian of the Sichote Alin (BRAGIN 1991) could not be confirmed. Reexamination of the locality with Spathian Albaillellacea by one of the authors (KOZUR) has shown that the radiolarites show strong reworking of older radiolarites and contain Permian-Triassic mixed faunas as known also from several Triassic radiolarites of Japan.

Especially important is the absence of Nassellaria in the Lower and Middle Scythian of Turkey,

but also in the Middle Scythian of Oregon (BLOOME & REED, 1992). As discussed below, the Nassellaria have evolved within the Upper Scythian from spicular radiolarians without shell. Nassellaria-like radiolarians from the Carboniferous are probably pylomate Entactinaria. For multicyrtide forms this explanation is not sure, but they are absent not only in nearly the entire Scythian (except rare occurrences of one multicyrtid radiolarian genus in the uppermost Scythian of Japan), but also in very rich radiolarian associations of the Permian.

Only in the Upper Scythian (Spathian), the first radiolarites were found in shale-radiolarite sequences of Panthalassa. However, still in that time the radiolarian fauna was not very diverse and consists mainly of Entactinaria (with and without shell, moderately diverse fauna). *Archaeosemantis* DUMITRICĂ, *Archaeothamnulus* DUMITRICĂ, *Cryptostephanidium* DUMITRICĂ, *Tiborella* DUMITRICĂ, KOZUR & MOSTLER, primitive *Parasepsagon* KOZUR & MOSTLER, primitive *Parentactinia* DUMITRICĂ, *Pentabelus* SUGIYAMA, primitive *Pseudostylosphaera* KOZUR & MOSTLER, *Stigmosphaerostylus* and *Tetrarhopalus* SUGIYAMA are present among the Entactinaria and all these genera are also present in the Anisian. Spumellarian and nassellarian Radiolaria are still rare, have a low diversity and are represented by primitive forms. Typical Oertlispongidae are still missing and the Spumellarian fauna is represented by primitive Pantanelliidae PESSAGNO (*Ellipsoxiphus* DUNIKOWSKI), primitive Actinommidae (*Pegoxystris* SUGIYAMA), *Plafkerium* ? *antiquum* SUGIYAMA and the above mentioned primitive Sponguracea (fam. et gen. inc., see chapter 3.).

The Spathian Nassellaria are represented by *Poulpus* DE WEVER, *Hozmadia* DUMITRICĂ, KOZUR & MOSTLER, and very rarely primitive *Hinedorcus* DUMITRICĂ, KOZUR & MOSTLER, *Tripedocorbis* DUMITRICĂ and *Zevius* SUGIYAMA are present, all also known from the Anisian. The first Nassellaria of the lower Spathian are primitive monocyrtid Sanfilippoellidae KOZUR & MOSTLER, 1979 (= Poulpidae DE WEVER, 1981, see KOZUR & MOSTLER, 1994). They often have a very loose shell and derived apparently from spicular Entac-

tinaria and not from the Carboniferous Pylentone-midae DEFLANDRE as formerly assumed. This is in agreement with the presence of a medullary shell in *Pylentonema* DEFLANDRE (CHENG, 1986, SU-GIYAMA, 1992). A medullary shell is absent in all Nassellaria, but present in many Entactinaria. Consequently, the similarities between the Sanfi-lippoellidae and the Pylentonemidae indicate only homeomorphy. The Pylentonemidae are therefore pylomate Entactinaria. This explains the total absence of Nassellaria during the Upper Carboniferous, Permian, Lower and Middle Scythian.

Also a part of the Spathian and younger Entactinaria evolved during the Spathian from spicular Entactinaria without shell. This is the case for *Parasepsagon leptaleus* SUGIYAMA, *Parentactinia nakatsugawaensis* SASHIDA, *P. ramosa* (SASHIDA), *P. okuchichibuensis* (SASHIDA), *Pentabelus furutanii* SUGIYAMA, *Pentactinorbis* ? *biacus* (SUGIYAMA), *P.* ? *crux*, (SUGIYAMA), *Tetrarhopalus itoigawai* SASHIDA and *Pseudostylosphaera kozuri* SUGIYAMA. But also *Spongostephanidium longispinosum* SASHIDA has a rather loose shell. For this reason, *Stigmosphaerostylus* is apparently the only Entactinaria genus with shell that survived the Permian-Triassic boundary.

The siliceous sponge spicules are as monotonous as the radiolarian fauna. They represent exclusively Hexactinellida (Lyssakida) with very low diversity. May be only one species is present.

The oldest Triassic siliceous sponge faunas of the Southern Alps and Northern Alps (Middle Triassic) consists always exclusively of Hexactinellida, independent from their age. They are always smooth hexactine spicules or smooth pentactine spicules with few hexactine spicules, like our fauna from the Lower Scythian of Turkey. Fully preserved Hexactinellida consist of dictyonal fused skeletons.

These hexactinellid sponges of the Triassic are pioneer faunas among the siliceous sponges at the beginning of a new siliceous sponge settlement after destruction of the former sponge communities due to tectonic or other events or by forming of a new marine sedimentation area. Only in an advanced stage of the pioneer settlement the first Demospongia appeared in these communities.

The Dienerian to lower Smithian siliceous sponges of Igdir (Turkey) are such a typical pioneer fauna after the strong faunal crises in the siliceous sponges near the P/T boundary. They are the oldest known Triassic siliceous sponge faunas after the Permian-Triassic biotic crisis. A similar siliceous sponge pioneer fauna in the western USA is of Spathian age (RIGBY & GOSNEY, 1983).

Acknowledgements

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Authors' addresses:

Dr. sc. H.einz W. Kozur, Rézsü u. 83, H-1029 Budapest, Hungary; Prof. Dr. Orhan Kaya, Dokuz Eylül University, Dept. Geolog. Engineer., 35102 Bornova-Izmir, Turkey; Univ.-Prof. Dr. Helfried Mostler, Institut für Geologie und Paläontologie der Universität, A-6020 Innsbruck, Austria.

Plate 1

All figured specimens are from sample K 7323, a thin-bedded black marly limestone within dark shales and siltstones from a Scythian block of a locality 500 NE of Igdir (NE of Bursa, northwestern Turkey); upper Dienerian or lower Smithian.

Figs. 1–6: *Stigmosphaerostylus turkensis* n. sp.; Fig. 1: holotype, x 100, rep.-no. 4-8-95/I-11; Fig. 2: x 150, rep.-no. 4-8-95/I-22; Fig. 3: x 100, rep.-no. 4-8-95/I-19; Fig. 4: opened specimen with visible spicular system, x 200, rep.-no. 4-8-95/I-24; Fig. 5: opened specimen with well visible spicular system, x 200, rep.-no. 4-8-95/I-12; Fig. 6: fragment with visible spicular system, x 250, rep.-no. 4-8-95/I-13.

Fig. 7:   Sponguracea, gen. et spec. indet., subspherical morphotype, x 200, rep.-no. 4-8-95/I-15.

Fig. 8:   Sponguracea, gen. et spec. indet., ellipsoidal morphotype, x 200, rep.-no. 4-8-95/I-16.

Fig. 9:   *Spinotriassocypris* sp., carapace from right, anterior end above, x 100, rep.-no. 4-8-95/I-25.
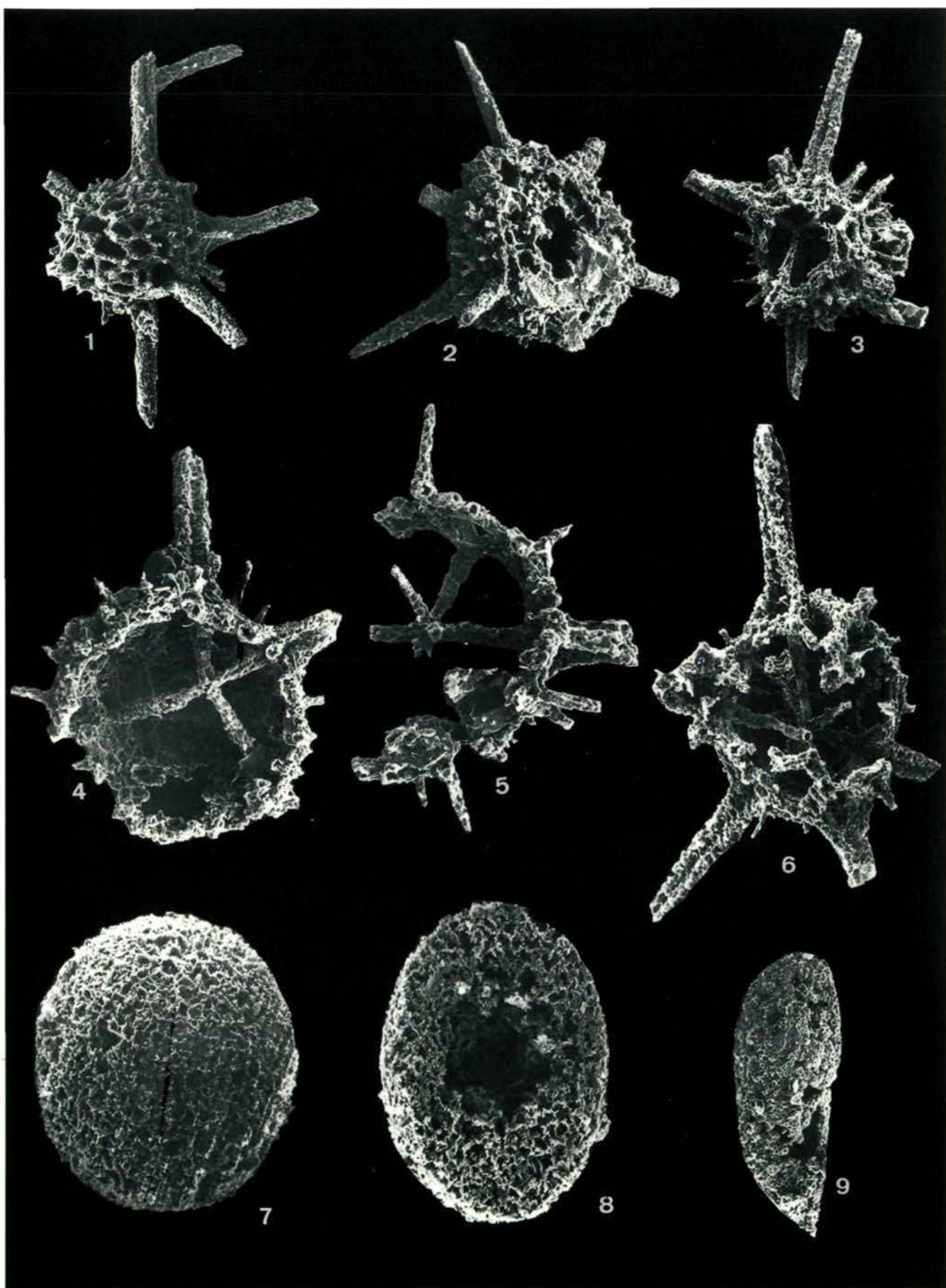
Plate 2

All figured specimens are from thin-bedded black marly limestone within dark shales and siltstones, from a Scythian block of a locality 500 NE of Igdir (NE of Bursa, northwestern Turkey). Figs. 1–9: Sample sample K 7323, upper Dienerian or lower Smithian; Figs. 10-12: sample K 7324, Dienerian.

Figs. 1–7: Pentactine spicule of Lyssakida; Fig. 1, x 100, rep.-no. 4-8-95/I-32; Fig. 2: x 100, rep.-no. 4-8-95/I-27; Fig. 3: x 170, rep.-no. 4-8-95/I-20; Fig. 4: x 200, rep.-no. 4-8-95/I-30; Fig. 5: x 200, rep.-no. 4-8-95/I-31; Fig. 6: x 200, rep.-no. 4-8-95/I-26; Fig. 7: specimen, in which the paratangential rays are curved in direction of the rhabd, x 100, rep.-no. 4-8-95/I-26.

Fig. 8: Hexactine spicule of Lyssakida, x 100, rep.-no. 4-8-95/I-29.

Fig. 9: *Neospathodus conservativus* (MÜLLER), Pa element, x 150, rep.-no. 4-8-95/I-18.

Fig. 10: *Clarkina procerocarinata* KOZUR, oblique lateral-upper view, x 100, rep.-no. 4-8-95/V-12.

Figs. 11–12: *Neospathodus dieneri* SWEET, Pa element; Fig. 10: x 150, rep.-no. 4-8-95/I-5; Fig. 11: x 150, rep.-no. 4-8-95/I-9.
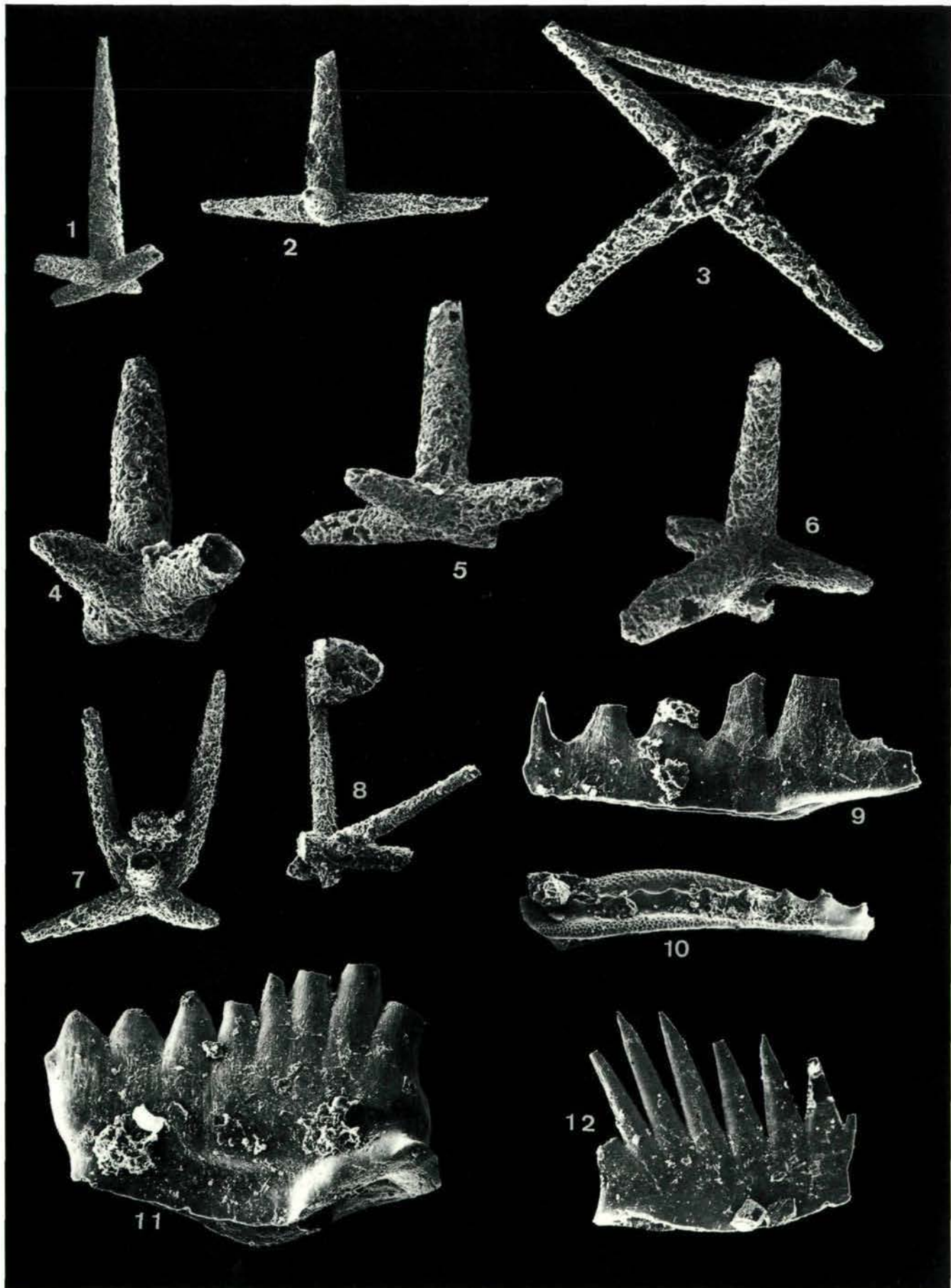
THE SYSTEMATIC POSITION OF *PSEUDOERTLISPONGUS* LAHM (RADIOLARIA) AND DESCRIPTION OF SOME NEW MIDDLE TRIASSIC AND LIASSIC RADIOLARIAN TAXA

Heinz W. Kozur

With 1 plate

Abstract:

Pseudoertlispongus LAHM is a transitional form between *Paroertlispongus* KOZUR & MOSTLER and *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER.

Paroertlispongus, Pseudoertlispongus and *Oertlispongus* appeared in successive order at the base of the Lower Anisian *Paroertlispongus diacanthus* Zone, at the base of the upper Subzone (*Yeharaia annulata* Subzone) of the uppermost Anisian *Spongosilicarmiger transitus* Zone and at the base of the Lower Ladinian *Spongosilicarmiger italicus* Zone (= base of *Reitziites reitzi* Zone s.str.)

One new genus, 7 new species and one new subspecies of Middle Triassic radiolarians and the Liassic genus *Liassobetracchium* n. gen. are described.

Zusammenfassung:

Pseudoertlispongus LAHM ist eine Übergangsform zwischen *Paroertlispongus* KOZUR & MOSTLER und *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER. *Paroertlispongus, Pseudoertlispongus* und *Oertlispongus* erscheinen in stratigraphischer Abfolge an der Basis der unteranisischen *Paroertlispongus diacanthus* Zone, in der oberen Subzone (*Yeharaia annulata* Subzone) der hoch-oberanisischen *Spongosilicarmiger transitus* Zone und an der Basis der unterladinischen *Spongosilicarmiger italicus* Zone (= Basis der *Reitziites reitzii* Zone).

Eine neue Gattung, 7 neue Arten und eine neue Unterart mitteltriassischen Radiolarien die liassische Gattung *Liassobetracchium* um werden beschrieben.

1. Introduction

KOZUR & MOSTLER (1994) regarded *Pseudoertlispongus* LAHM, 1984 as a junior synonym of *Paroertlispongus*. At that time, only one species of *Pseudoertlispongus* was known that occurred in the middle Fassanian together with advanced *Paroertlispongus* KOZUR & MOSTLER, advanced *Oertlispongus* DUMITRICĂ, KOZUR & MOSTLER, *Baumgartneria* DUMITRICĂ and *Falcispongus* DUMITRICĂ. Shell sculpture and arrangement of the spines on the shell of *Pseudoertlispongus* correspond to *Paroertlispongus* and also the round cross section of the main polar spine throughout its length is typical for Paroertlispongus. The only

difference is a slightly curved posterior end of the main polar spine. This last feature is transitional to *Oertlispongus* that has a recurved main polar spine with a short straight part and a long recurved part. However, the previously known distribution of *Pseudoertlispongus* with first appearance after the first appearance of *Oertlispongus* did not favour the possibility that *Pseudoertlispongus* is a transitional form between *Paroertlispongus* and *Oertlispongus*.

Now we have found rich *Pseudoertlispongus* faunas before the first appearance of *Oertlispongus* in Hungary as well as in Sicily. Therefore, the formerly known occurrence of *Pseudoertlispongus weddigei* was only the uppermost range of

Pseudoertlispongus together with advanced *Oertlispongus* that ranges, however, up to the Longobardian. The first appearance of *Paroertlispongus*, *Pseudoertlispongus* and *Oertlispongus* is therefore in clear stratigraphic order, independently from the fact that the primitive Oertlispongidae co-occur with advanced ones. The oldest known occurrence of *Paroertlispongus* is in the upper Lower Anisian *Paroertlispongus diacanthus* Zone. There, only forms with long, slender, in their middle part not widened main polar spine occur, and the opposite polar spine is not much different. Advanced *Paroertlispongus* with widening of the main polar spine in or after its mid-length appear in the Upper Anisian *Tetraspinocyrtis laevis* Zone from the *Paraceratites* trinodosus Zone of the ammonoid zonation. They ranges up to the upper Fassanian.

Pseudoertlispongus with terminally slightly curved main polar spine appeared in the uppermost Anisian upper Subzone (*Yeharaia annulata* Subzone) of the *Spongosilicarmiger transitus* Zone. With very slight changes, this genus ranges up to the upper Fassanian.

Oertlispongus with recurved main polar spine begins at the base of the Ladinian *Spongosilicarmiger italicus* Zone (base of the *Reitziites reitzi* zone s.str. in the ammonoid zonation). The oldest *Oertlispongus* species, *O. primus* n. sp., is a primitive form with a long straight part of the main polar spine that is only a little shorter than or as long as the curved part that is only very little recurved. The bent is already slightly flattened (oval cross section) as typical for several *Oertlispongus* species, but never present in *Paroertlispongus* and *Pseudoertlispongus*. This genus underwent a rapid evolution and advanced forms with very short straight part of the main spine occur from the middle Fassanian up to the Middle Longobardian. Contemporaneous with *O. primus*, a closely related form appeared, in which, however, the inward curved part is short, the bent of the main spine is strongly flattened and on its outer side slightly widened. These forms represent the oldest *Falcispongus*, *F. zapfei* n. sp., which is the ancestral form of the advanced oertlispongids with strongly differentiated main polar spine that characterize the Tethyan and partly also the Circum-Pacific Ladinian and Cordevolian.

In the present paper, the stratigraphically very important species from the transitional field of *Paroertlispongus*, *Oertlispongus* and *Falcispongus* are described. Furthermore some other new species and genera are described that are used in stratigraphical papers without systematic part, to avoid the use of nomina nuda.

2. Systematic part

Subclass Radiolaria MÜLLER, 1858
Order Polycystida EHRENBERG, 1838
Suborder Entactinaria KOZUR & MOSTLER, 1982
Superfamily Palaeoscenidiacea RIEDEL, 1967
emend. KOZUR & MOSTLER, 1982
Family Eptingiidae DUMITRICĂ, 1978

Genus *Cryptostephanidium* DUMITRICĂ, 1978

Type species: *Cryptostephanidium cornigerum* DUMITRICĂ, 1978

Cryptostephanidium sugiyamai n. sp.

Derivatio nominis: In honour of Prof. Dr. KAZUHIRO SUGIYAMA, Nagoya, for his excellent work on Lower and Middle Triassic radiolarians.
Holotypus: The specimen figured by SUGIYAMA (1992), Fig. 13-3; rep.-no. ESN 146172.
Locus typicus: Mt. Kinkazan section of Gifu, Gifu Prefecture, central Japan.
Stratum typicum: Bedded cherts, sample KIN 61 (see SUGIYAMA, 1992, Fig. 2), Lower Anisian *Hozmadia gifuensis* Zone.
Diagnosis: Pore frames with verrucose to irregular spiny surface. The three main spines are of unequal length. Their proximal third to half is three-bladed, their distal half is round.
Description: Shell small, subspherical. The surface of the pore frames is verrucose or covered with very small, irregular, partly oblique spines. Pores moderately large, mostly pentagonal. The three

main spines are situated in continuation of spines of the entactinarian spicular system. Their width decreases gradually from the base to the pointed needle-like distal end. The spine A is longer than the two spines L. the proximal third to half of the main spines is three-bladed. The furrows between the blades are wide, at the base of the spines deep, but they become shallow in distal direction. The distal half to 2/3 of the main spines has a circular cross section and no blades and furrows are present.

Measurements:

Diameter of shell: 85–100 µm

Length of main spines: 60–95 µm

Maximal width of the main spines: 20–25 µm

Occurrence: Common in the Lower Anisian of Karaburun peninsula (western Turkey) and in Japan.

Remarks: The Turkish material is rich in specimens, but not well preserved. Therefore, the specimen figured by SUGIYAMA (1992) was chosen as holotype.

Cryptostephanidium sugiyamai n. sp. is a transitional form between *Spongostephanidium* DUMITRICĂ, 1978 emend. KOZUR, KRAINER & MOSTLER, this volume, and *Cryptostephanidium* DUMITRICĂ, 1978. The proximal third to half of the main spines is already tricarinate as in *Cryptostephanidium*, the distal half to 2/3 of the main spines is needle-like with round cross section as in *Spongostephanidium*.

In the younger *Cryptostephanidium* species nearly the entire main spines are tricarinate. In the otherwise similar *C. verrucosum* DUMITRICĂ, 1978, the three main spines have equal length.

Suborder Spumellaria EHRENBERG, 1875
Superfamily Actinommacea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1979
Family Pantanelliidae PESSAGNO, 1977

Genus *Liassobetraccium* n. gen.

Type species: *Betraccium bavaricum* KOZUR & MOSTLER, 1990

Derivatio nominis: According the similarity to *Betraccium* PESSAGNO and the occurrence in the Liassic.

Diagnosis: Cortical shell subspherical with high and coarse pore frames. The pores are very large, but irregular in size and shape. Most pores are triangular and tetragonal, but some pentagonal pores may be also present. Some pores may be divided by fragile secondary pore frames. Vertices of the pore frames with distinct nodes and spines. The three stout, three-bladed main spines are twisted or untwisted, equidistant and of the same size. Medullary shell present.

Occurrence: Hettangian of the Tethys.

Assigned species:

Betraccium bavaricum KOZUR & MOSTLER, 1990

Betraccium hettangicum KOZUR & MOSTLER, 1990

Betraccium inaequiporatum KOZUR & MOSTLER, 1990

Betraccium verticispinosum KOZUR & MOSTLER, 1990

Remarks: *Betraccium* PESSAGNO, 1979, is a very common Upper Norian and Rhaetian genus both in the Tethys and in the Circum-Pacific realm. It suddenly disappeared at the base of the Liassic (CARTER, 1993). However, there are some closely related species in the Hettangian that have been assigned to *Betraccium* by KOZUR & MOSTLER (1990). In contrast to typical Triassic *Betraccium* species, in all these species the pore frames encloses pores of different size and shape. In *Betraccium* all pores have the same size and pentagonal or hexagonal outline. In the Liassic forms the pore outline is in general triangular or tetragonal and only subordinately pentagonal outline of the pores is present. These Liassic species group is separated as *Liassobetraccium* n. gen.

Superfamily Sponguracea HAECKEL, 1862
emend. KOZUR & MOSTLER, 1981
Family Oertlispongidae KOZUR & MOSTLER,
1980 (in DUMITRICĂ et al., 1980)

Genus *Falcispongus* DUMITRICĂ, 1982

Type species: *Falcispongus falciformis* DUMITRICĂ, 1982

Falcispongus zapfei n. sp.
(Pl. 1, Fig. 10)

Derivatio nominis: in honour of Prof. emer. H. ZAPFE, Vienna, for his outstanding contributions to the Triassic stratigraphy.

Holotypus: The specimen on Pl. 1, Fig. 10; rep.-no. 14-4-94/V-5

Locus typicus: Outcrop ca. 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy).

Stratum typicum: Basal 20 cm of red, strongly siliceous, marly limestones, sample Ko 5. Very base of the Ladinian, base of the *S. italicus* Zone.

Material: 2 specimens.

Diagnosis: The perpendicularly inward bent distal part of the main polar spine is considerably shorter than straight axial proximal part. Main polar spine at the bent flattened, with small widening at the outer side directly before the bent.

Description: Straight axial proximal part of the main polar spine in its upper part flat, with small widening at its outer side directly before the bent. The perpendicularly inward bent distal part is distinctly shorter than the straight part of the main polar spine. It is not recurved. Shell not preserved.

Measurements:

Length of the straight part of the main polar spine: 300–360 μm

Width of the straight part of the main polar spine at its proximal end (above the conical part that was originally within the shell): 30–33 μm

Width of the straight part of the main polar spine directly before the bent: 40–53 μm

Length of the inward curved part of the main polar spine: 160–200 μm

Occurrence: Lower part of *Oertlispongus primitivus* Subzone of the *S. italicus* Zone of western Sicily (lower Fassanian).

Remarks: *Falcispongus zapfei* n. sp. is the most primitive *Falcispongus* species. All other lower Ladinian species of this genus have a long inward curved and mostly also recurved distal part that is longer than the straight proximal part. The widening at the outer side of the distal end of the straight part of the main polar spine or (and) at the bent is more pronounced in the other *Falcispongus* species.

F. zapfei is similar both to *Pseudoertlispongus mostleri siciliensis* n. subsp. and to *Oertlispongus primus* n. sp. The main polar spine of *Pseudoertlispongus mostleri siciliensis* is not flattened near the bent and no widening at the outer side of the straight part of the main polar spine directly below the bent is present. In *Oertlispongus primus* n. sp., the inward curved part is about as long as the straight part. Apparently, at the base of the Ladinian both the first primitive *Oertlispongus* and the first primitive *Falcispongus* have evolved from *Pseudoertlispongus* of the *P. mostleri* group.

Genus *Oertlispongus*
DUMITRICĂ, KOZUR & MOSTLER, 1980

Type species: *Oertlispongus inaequispinosus* DU-MITRICĂ, KOZUR & MOSTLER, 1980

Oertlispongus primus n. sp.
(Pl. 1, Fig. 9)

Derivatio nominis: Oldest known true *Oertlispongus* species.

Holotype: The specimen on Pl. 1, Fig. 9; rep.-no. 14-4-94/V-24

Locus typicus: Outcrop ca. 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy).

Stratum typicum: Basal 20 cm of red, strongly siliceous, marly liMestones, sample Ko 5. Very base of the Ladinian, base of the *S. italicus* Zone.

Material: 5 specimens.

Diagnosis: Straight proximal part of the main polar spine long, only a little shorter than or as long as the nearly perpendicularly inward curved part that is only insignificantly recurved.

Description: The straight axial proximal part of the main polar spine is long for the genus and only somewhat shorter than the inward curved part. In the proximal part the cross section of the main polar spine is round, but in its upper part and in the bent the main polar spine is flattened and has an oval cross section. The inward curved part lies nearly perpendicular to the straight axial part; it is only somewhat longer than or as long as the axial

straight proximal part. The inward curved part is nearly not recurved. Shell not preserved.

Measurements:

Length of the straight axial proximal part of the main polar spine: 280–295 µm

Width of the straight axial proximal part of the main polar spine at its proximal end (above the conical part that was originally within the shell): 27–29 µm

Width of the main polar spine directly before the bent: 39–43 µm

Length of the inward curved part of the main polar spine: 280–305 µm

Occurrence: Lower part of *Oertlispongus primitivus* Subzone of the *S. italicus* Zone. Basal part of Ladinian. Hungary and Sicily (Italy).

Remarks: *Oertlispongus primus* n. sp. is the oldest and most primitive *Oertlispongus* species. It has transitional character to *Pseudoertlispongus mostleri siciliensis*. It is distinguished from all *Pseudoertlispongus* species by its longer, strongly inward curved part that is nevertheless not or only a little longer than the straight axial proximal part of the main polar spine. Additionally, the main polar spine is flattened near the bent.

In all other *Oertlispongus* species the inward bent part is considerably longer than the straight proximal part and, except of few undescribed forms from the lowermost Ladinian, strongly recurved.

Falcispongus nicorae n. sp. displays a shorter inward bent part and a slight widening is present at the outer side of the bent.

Genus *Paroertlispongus* KOZUR & MOSTLER, 1981

Type species: *Paroertlispongus multispinosus* KOZUR & MOSTLER, 1981

Remarks: Three *Paroertlispongus* species occur in sample Ko 5 from the basal *S. italicus* Zone of Sosio Valley, Sicily (Italy), that are *P. multispinosus* KOZUR & MOSTLER, 1981 (Pl. 1, Fig. 1), *P. rarispinosus* KOZUR & MOSTLER, 1981 (Pl. 1, Fig. 2) and *P. chinensis* (FENG, 1992) (Pl. 1, Fig. 3). The first two species are only represented by isolated main polar spines, a very typical preservation for Oertlispongidae. The main polar spine of *P. multispinosus* is widest after its midlength. The main polar spine of *P. rarispinosus* is cylindrical in its proximal half and becomes needle-like towards its distal end. *P. chinensis* has several small, low ribs at the base of both polar spines.

Genus *Pseudoertlispongus* LAHM, 1984

Type species: *Pseudoertlispongus weddigei* LAHM, 1984

Occurrence: *Yeharaia annulata* Subzone of the *Spongosilicarmiger transitus* Zone (upper Illyrian) of the Tethys.

Remarks: *Pseudoertlispongus* has the same distribution of the second order spines on the spongy shell as *Paroertlispongus*, but the distal end of the main polar spine is curved. The straight part of the main polar spine is considerably longer than the curved part. In *Oertlispongus* the distribution of the second order spines is different from *Paroertlispongus* and *Pseudoertlispongus*, and the main spine is recurved. The straight part of the main polar spine is shorter than the curved part. By the presence of a distally somewhat curved spine, *Pseudoertlispongus* is a transitional form between *Paroertlispongus* and *Oertlispongus*. It appears considerably later than the first *Paroertlispongus*, but distinctly before the first *Oertlispongus*.

Pseudoertlispongus angulatus n. sp.
(Pl. 1, Figs. 4, 5)

Derivatio nominis: According to the abruptly inward curved distal end of the main polar spine.

Holotypus: The specimen on Pl. 1, Fig. 4; rep.-no. 16-2-95/II-104.

Locus typicus: Torrente San Calogero section (see CATALANO, DI STEFANO & KOZUR, 1991).

Stratum typicum: Basal 10 cm of the gray radiolarite directly above the Changxingian red deepwater clay. Uppermost Anisian *Y. annulata* Subzone of the *S. transitus* Zone.

Material: 12 specimens.

Diagnosis: The main polar spine is widest immediately before the abrupt, angular bent in its distal third.

Description: The main polar spine is large. Its width increases gradually and slowly until the sharp angular bent in the distal third of the main polar spine. The straight, inward directed distal part of the main polar spine has different length and the angle with the straight axis of the main polar spine varies, but it is not larger than 45°. Only this inward directed part becomes narrower towards the pointed distal end. Shell not preserved.

Measurements:

Length of the main polar spine: 440–510 µm

Length of the straight axial part of the main polar spine: 350–370

Length of the inward bent part: 100–150 µm

Width of the proximal part of the main polar spine (above the conical part that was originally situated inside the shell): 30 µm

Width directly before the bent of the main polar spine: 35–46 µm

Occurrence: Uppermost Anisian (? and lowermost Ladinian) of western Sicily.

Remarks: In the other two known *Pseudoertlispongus* species, *P. weddigei* LAHM, 1984 and *P. mostleri* n. sp., the bent is gently curved. In *P. weddigei* additionally the main spine becomes narrower directly before the bent.

Pseudoertlispongus mostleri n. sp.
(Pl. 1, Figs. 6, 7)

1994   *Paroertlispongus weddigei* (LAHM, 1994) – KOZUR & MOSTLER, p. 69-70, Pl. 12, Figs. 12-14

Derivatio nominis: In honour of Univ.-Prof. Dr. H. MOSTLER for his outstanding contributions to the Triassic radiolarian research.

Holotypus: The specimen on Pl. 1, Fig. 6; 14-4-94/V-3.

Locus typicus: Outcrop ca. 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy). Stratum typicum: Basal 20 cm of red, strongly siliceous, marly limestones, sample Ko 5. Very base of the Ladinian, base of the *S. italicus* Zone.

Material: 35 specimens.

Diagnosis: Shell spongy with numerous by-spines that are not concentrated to any part of the shell. Main polar spine cylindrical, widest directly before or at the bent. The bent is gradual and rounded.

Description: The spherical spongy shell consists of several layers. Its surface is covered by numerous needle-like by-spines that start in well preserved forms from node-like elevations. The main polar spine is very long and mostly the only preserved part of a specimen. It is cylindrical and widest directly before the bent or at the bent. The bent is gradually rounded. The inward-curved distal part of the main polar spine is short, its angle with the long axial straight part of the main polar spine is around 45°, but in the subspecies *P. mostleri siciliensis* between 45° and nearly 90°. The second polar spine opposite or somewhat obliquely opposite to the main polar spine is long, needle-like, but rarely preserved.

Measurements: See under the subspecies.

Occurrence: Uppermost Anisian *Y. annulata* Subzone of the *S. transitus* Zone and lower Ladinian *S. italicus* Zone.

Remarks: *Pseudoertlispongus mostleri* is the transition form between *Pseudoertlispongus* and *Oertlispongus*. The spongy shell with nodes and by-spines on the entire surface corresponds to *Paroertlispongus multispinosus*. The main polar spine is also similar, but distally inward curved.

   In *Oertlispongus primus* n. sp., the oldest *Oertlispongus* species, the early perpendicularly inward curved part is longer than or as long as the straight axial part of the main polar spine.

Pseudoertlispongus mostleri mostleri n. subsp.
(Pl. 1, Fig. 6)

Holotypus, locus typicus and stratum typicum: As for the species.

Material: 31 specimens.

Diagnosis: With the character of the species. The distal, inward bent part of the main polar spine is always short and its angle with the axial straight part of the main polar spine is not larger than 45°.

The main polar spine is broadest directly before the bent.

Measurements:

Diameter of shell: 180–267 µm

Length of the main polar spine: 350–430 µm

Width of the main polar spine at its proximal end (outside the shell or outside the conical part, if the shell is not preserved: 20–35 µm

Width of the main polar spine directly before the bent: 26–50 µm

Length of the inward curved distal part of the main polar spine: 50–95 µm

Length of the by-spines: 10–50 µm

Occurrence: Uppermost Anisian *Y. annulata* Subzone of the *S. transitus* Zone and Lower Fassanian *S. italicus* Zone of Hungary, Southern Alps and Sicily (Italy).

Remarks: In *Pseudoertlispongus mostleri siciliensis* n. subsp., the main polar spine is widest at the bent and the distal part is stronger inward curved.

Pseudoertlispongus mostleri siciliensis n. subsp.
(Pl. 1, Fig. 7)

Derivatio nominis: According to the occurrence in Sicily.

Holotype: The specimen on Pl. 1, Fig. 7; rep.-no.: 14-4-94/V-2.

Locus typicus and stratum typicum: As for the species.

Material: 4 specimens.

Diagnosis: With the character of the species. Main polar spine widest at the bent or of the same width throughout its straight axial part. Inward bent strong, partly nearly perpendicular to the straight axial part of the main spine.

Measurements:

Length of the main polar spine: 500–520 µm

Width of the main polar spine at its proximal end (after the conical part, that was originally inside the shell): 40–47 µm

Width of the main polar spine at the bent: 43–47 µm

Length of the inward curved distal part of the main polar spine: 133–147 µm

Occurrence: Upper part of the uppermost Anisian *Y. annulata* Subzone of the *S. transitus* zone and

lower part of *Oertlispongus primitivus* Subzone of the *S. italicus* Zone.

Remarks: *Pseudoertlispongus mostleri mostleri* n. subsp. has a fewer inward bent distal part of the main polar spine that is widest directly before the bent.

In *Oertlispongus primus* n. sp. the inward part of the main polar spine is somewhat longer than or as long as the straight axial part of the main polar spine.

Superfamily Trematodiscacea HAECKEL, 1862 emend. KOZUR & MOSTLER, 1979
Family Relindellidae KOZUR & MOSTLER, 1980 (in DUMITRICĂ et al., 1980)

Genus *Pentaspongodiscus* KOZUR & MOSTLER, 1979

Type species: *Pentaspongodiscus tortilis* KOZUR & MOSTLER, 1979

Pentaspongodiscus lahmi n. sp.

1984   *Pentaspongodiscus anisicum* KOZUR & MOSTLER 1981 – LAHM, p. 57, Pl. 10, Fig. 1

Derivatio nominis: In honour of Dr. B. LAHM, München, who firstly found first this species.

Holotypus: The specimen figured by LAHM (1984) on Pl. 10, Fig. 1 under *Pentaspongodiscus anisicus* KOZUR & MOSTLER, 1981; rep.-no. Prot. 3623.

Locus typicus: Section Rec. A, 2.5 km SE of Recoaro, in the Val di Creme.

Stratum typicum: Limestone with siliceous nodules about 40 cm above the beginning of the pelagic limestones, sample Rec. A 9. Lower *S. italicus* Zone (Lower Ladinian).

Material: 23 specimens.

Diagnosis: The five untwisted tricarinate main spines are slender and shorter than the shell diameter.

Description: The discoidal shell is large compared with the length of the main spines. Its equatorial outline is round. It is spongy with *Alievum* pattern of the outer pore frames. Distinct small nodes

are present on the slightly elevated vertices. Five fragile short rays originate in all vertices. The five slender main spines are tricarinate, with a needle-like, round distal prolongation. They are untwisted and always shorter than the shell diameter.

Measurements:
Diameter of shells: 150–167 µm
Length of the main spines: 100–133 µm
Width of the main spines at their base: 23–25 µm

Occurrence: Lower Ladinian *S. italicus* Zone of Hungary and Italy.

Remarks: LAHM (1984) assigned this species to *Pentaspongodiscus anisicus* KOZUR & MOSTLER, 1981. However, this Upper Anisian species (ancestor of *P. lahmi*) has a pentagonal equatorial outline of the shell and the robust, long main spines are distinctly longer than the shell diameter.

Suborder Nassellaria EHRENBERG, 1875
Family Hinedorcidae KOZUR & MOSTLER, 1981

Genus *Picapora* KOZUR & MOSTLER, 1981

Type species: *Picapora robusta* KOZUR & MOSTLER, 1981

***Picapora fassanica* n. sp.**

Derivatio nominis: According to the occurrence in the Fassanian.

Holotypus: The specimen figured by GORIČAN & BUSER (1990), Pl. 11, Fig. 1.

Locus typicus: 1.5 km north of Zaklanec near Horjul at the Zaklanec-Koreno road (southern part of the Slovenian Basin); see GORIČAN & BUSER, 1990, Fig. 1.

Stratum typicum: Cherty limestone below volcanics, sample Gr 10 (see GORIČAN & BUSER, 1990, Fig. 2).

Material: 23 specimens.

Diagnosis: A *Picapora* with small vertical horn.

Description: Cephalis subspherical (somewhat broader than high) with small pores that are mostly closed by a layer of microgranular silica; surface slightly verrucose. The apical horn is stout, tricari-

nate, with deep and broad furrows between the high and narrow blades. A distinct, but rather small and short, carinate vertical horn is present. Thorax larger than cephalis, with the same surface structure and mostly closed small pores. It has the shape of a cone frustum or it is subspherical. Its wide aperture is closed by a fragile thin layer with small pores that is often destroyed. The three feet are stout, moderately long, tricarinate. They run from the distal part of the cephalis on the surface of the thorax and are free only beyond the thorax. Cephalic spicular system with Mb, A, V, 2 L, D, 2 l. The spines A and V continue outside the shell as apical horn and horn V, whereas D and 2 L continue as feet.

Measurements:
Height of cephalis: 30–40 µm
Width of cephalis: 50–55 µm
Height of thorax: 50–60 µm
Width of thorax: 70–85 µm
Length of the apical horn: 40–45 m
Length of the free part of the feet: 50-55 µm

Occurrence: Fassanian of Slovenia, Hungary and Italy.

Remarks: The Julian *Picapora robusta* KOZUR & MOSTLER, 1981 has a very big vertical horn.

Family Triassocampidae
KOZUR & MOSTLER, 1981

Genus *Praeyeharaia* n. gen.

Type species: *Yeharaia transita* KOZUR & MOSTLER, 1994

Derivatio nominis: According to the ancestral position to *Yeharaia* NAKASEKO & NISHIMURA, 1979

Diagnosis: Test multicyrtid, conical. Cephalis conical, smooth with small apical horn. Thorax a little broader, but in general shorter than the cephalis, ring-like or hoop-like, with nodes or a ring of nodes; pores small, mainly closed. Abdomen cylindrical or hoop-like, nodose, with small, partly open pores. The postabdominal segments are in general inverted conical with a smooth, in the proximal segments slightly nodose proximal ring. The distal part of these segments is nodose. Below

the proximal ring a ring of rather large pores is present. In the distal part of the postabdominal segments a second, often incomplete pore ring is present. The proximal two postabdominal segments may be hoop-like, with indistinct proximal ring. Cephalic spicular system with A, V, 2 L, D, 2 l. Only spine A continues outside the shell wall as short apical spine. Sometimes also a tiny spine is present in prolongation of D.

Occurrence: Uppermost Anisian *S. transitus* Zone and Lower Ladinian *S. italicus* Zone.

Assigned species:

Yeharaia transita KOZUR & MOSTLER, 1994

Yeharaia japonica NAKASEKO & NISHIMURA, 1979

Yeharaia lata KOZUR & MOSTLER, 1994

Remarks: *Yeharaia* NAKASEKO & NISHIMURA, 1979, has a long apical spine and an inflated thorax and the postabdominal segments (except the first one) have only one ring of pores. *Triassocampe* DUMITRICĂ, KOZUR & MOSTLER, 1980 has no apical spine.

Praeyeharaia n. gen. is transitional between *Yeharaia* and *Triassocampe*. *Praeyeharaia* species have been in previous paper partly assigned to *Yeharaia*, partly to *Triassocampe*.

3. Stratigraphic evaluation

The Oertlispongidae are the most important Ladinian radiolarian guideforms of the Tethys. In previous studies, *Paroertlispongus* was found in the Illyrian and Fassanian, and rich *Oertlispongus* faunas with *O. inaequispinosus primitivus* KOZUR & MOSTLER were found in the lower Fassanian lower *Reitziites reitzi* ammonoid zone s. str. (*O. inaequispinosus primitivus* Subzone of the *S. italicus* radiolarian zone). Despite the fact that *Paroertlispongus* was regarded as the forerunner of *Oertlispongus* (KOZUR & MOSTLER, 1981), the transition forms between both genera, and the immediate forerunner of *Falcispongus* were not found.

In the upper subzone of the *S. italicus* Zone both advanced *Oertlispongus* with very short proximal straight part of the main polar spine (e.g. *O. inaequispinosus inaequispinosus*) and typical *Falcispongus* were found.

Investigations of rich further material of sample 100 D (*Kellnerites felsoeoersensis* ammonoid zone) from the Felsőőrs section in the Balaton Highland (Hungary) and investigations near the base of the *Reitziites reitzi* Zone in the Balaton Highland, Southern Alps and in Sicily have yielded the complete transitional series from *Paroertlispongus* to *Oertlispongus*. *Pseudoertlispongus mostleri*, n.sp. a transitional form between *Paroertlispongus* and *Oertlispongus* appeared near the base of the *Kellnerites felsoeoersensis* ammonoid zone. The radiolarian fauna of this level belongs to the upper subzone (*Yeharaia annulata* Subzone) of the *S. transitus* Zone. Beside of Ladinian elements, as *Eptingium manfredi manfredi* DUMITRICĂ, *Pseudoertlispongus mostleri* n. sp., *Triassocampe deweveri* (NAKASEKO & NISHIMURA), *T. scalaris* DUMITRICĂ, KOZUR & MOSTLER and *Yeharaia annulata* NAKASEKO & NISHIMURA, this fauna contains still dominating Anisian elements, listed in KOZUR, KRAINER & MOSTLER (this volume). Consequently, this fauna was assigned by KOZUR (1995) to the uppermost Anisian. It has, however, transitional character to Ladinian radiolarian faunas, but advanced Oertlispongidae, which dominate in the entire Ladinian, are still missing. They begin near the base of the *Reitziites reitzi* ammonoid zone at the base of the *S. italicus* radiolarian zone. There, not only *Pseudoertlispongus mostleri* n.sp. is present, but also the first *Oertlispongus* s. str. in which the lateral curved (and mainly distinctly recurved) distal part of the main polar spine is at least as long as the proximal straight part. In typical *Oertlispongus*, this distal part is strongly recurved and considerably longer than the straight proximal part. In *Oertlispongus primus* the inward curved part is about as long as the proximal straight part and it is therefore a perfect transition form between *Pseudoertlispongus mostleri siciliensis* and *Oertlispongus inaequispinosus*. In the same level also the first *Falcispongus*, *F. zapfei*, appeared. This form also derived from *Pseudoertlispongus mostleri siciliensis*, the inward curved part is still as short as in this

species and considerably shorter than the straight proximal part of the main polar spine, but it is already strongly flattened near the bent, and directly below the bent a small widening is present at the outer side of the straight part of the main polar spine. By this can be demonstrated that *Falcispongus* did not evolve from *Oertlispongus*, but directly from *Pseudoertlispongus*.

Throughout the Ladinian, the primitive Oertlispongidae continue beside the advanced forms. *Pseudoertlispongus mostleri* n.sp. and *P. angulatus* n.sp. are the only Oertlispongidae with differentiated main polar spine (inward curved distal part) in the uppermost Illyrian *Y. annulata* Subzone of the *S. transitus* Zone. Advanced Oertlispongidae with short straight proximal part of the main polar spine and long, recurved distal part are not yet present. These forms appeared at the base of the *S. italicus* Zone. In a very short interval these advanced forms are only represented by transitional forms to the primitive Oertlispongidae with very long straight proximal part of the main polar spine, but a little later already forms with very long recurved distal part and distinctly short straight proximal part of the main polar spine are present. However, the primitive Oertlispongidae still continue in this stratigraphic level, e.g. *Paroertlispongus*, *Pseudoertlispongus* and primitive *Oertlispongus*. In the Lower Longobardian highly advanced Oertlispongidae with strongly differentiated spines occur (genera *Pterospongus*, *Bogdanella* etc.), but *O. inaequispinosus* from the Fassanian continued into this level. Therefore, for the subdivision of the Middle Triassic radiolarian faunas, the first appearance of a certain taxon is very important and the exact age is indicated by the most advanced forms within a phylogenetic cline.

Acknowledgements

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Author's address:
Dr. sc. H.einz W. Kozur, Rézsü u. 83, H-1029 Budapest, Hungary.

Plate 1

If not otherwise indicated, all figured specimens are from sample Ko 5 (basal 20 cm of red, strongly siliceous, marly limestones; very base of the Ladinian, base of the *S. italicus* Zone) in an Scythian to Ladinian section ca. 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily, Italy (location see GULLO & KOZUR, 1993).

Fig. 1:   *Paroeertlispongus multispinosus* KOZUR & MOSTLER, 1981, isolated main polar spine, x 130, rep.-no. 14-4-94/V-10.

Fig. 2:   *Paroertlispongus rarispinosus* KOZUR & MOSTLER, 1981, isolated main polar spine, x 150, rep.-no. 14-4-94/V-7

Fig. 3:   *Paroertlispongus chinensis* (FENG, 1992), x 100, rep.-no. 14-4-94/V-8

Figs. 4, 5: *Pseudoertlispongus angulatus* n.sp., x 200, sample SCK II/93, lowermost 10 cm of gray radiolarite directly above Changxingian red deep-water clay, *Yeharaia annulata* Subzone of *Spongosilicarmiger transitus* Zone, uppermost Anisian, Torrente San Calogero section (see CATALANO et al., 1991); Fig. 4: holotype, rep.-no. 16-2-95/II-104; Fig. 5: rep.-no. 16-2-95/II-106.

Fig. 6:   *Pseudoertlispongus mostleri mostleri* n. sp., holotype, x 200, rep.-no. 14-4-94/V-3.

Fig. 7:   *Pseudoertlispongus mostleri siciliensis* n. subsp., holotype, x 200, rep.-no. 14-4-94/V-2.

Fig. 8:   *Eptingium manfredi manfredi* DUMITRICĂ, 1978, x 130, rep.-no. 14-4-94/V-9.

Fig. 9:   *Oertlispongus primus* n. sp., holotype, x 145, rep.-no. 14-4-94/V-24.

Fig. 10   *Falcispongus zapfei* n. sp., holotype, x 150, rep.-no. 14-4-94/V-5.

Fig. 11:   *Triassocampe scalaris baloghi* KOZUR & MOSTLER, 1994, x 300, rep.-no. 14-4-94/V-6.