Tommotiids from the early Cambrian (Series 2, stage 3) of Morocco and the evolution of the tannuolinid scleritome and setigerous shell structures in stem group brachiopods

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Abstract: An assemblage of tannuolinid sclerites is described from the Amouslek Formation (Souss Basin) of the Anti-Atlas Mountains in Morocco. The assemblage contains two species, *Tannuolina maroccana* n. sp. which is represented by a small number of mitral and sellate sclerites and *Micrina* sp., represented by a single mitral sclerite. *Tannuolina maroccana* differs from other species of the genus in the presence of both bilaterally symmetrical and strongly asymmetrical sellate sclerites. This observation suggests that the scleritome of *Tannuolina* was more complex than previously thought and that this tommotiid may have held a more basal position in the brachiopod stem group than previously assumed. The shell structure of both *T. maroccana* and *Micrina* sp. is well preserved and exhibits two fundamentally different sets of tubular structures, only one of which was likely to contain shell penetrating setae. Based on these observations the structure of the tannuolinid shell is discussed and its implications for the evolution of tubular microstructures in stem and crown

group brachiopods is analyzed.

Key words: Early Cambrian, Morocco, Tannuolinids, Scleritome, Shell structure, Shell penetrating setae

DURING the Cambrian period, skeletal fossils appear for the first time in great diversity and abundance (Bengtson 2004; Maloof *et al.* 2010; Kouchinsky *et al.* 2012). Many of the oldest Cambrian fossils exhibit unusual character combinations and have often been regarded as biologically and phylogenetically problematic (Bengtson *et al.* 1990). However, in recent years many of the problematic Cambrian fossils have been suggested to represent stem groups or early members of modern shell-bearing phyla such as the Mollusca (Conway Morris and Peel 1995; Vinther and Nielsen 2005) and Arthropoda (Chen *et al.* 1995; Skovsted and Peel 2001).

Tommotiids are an important group of problematic Cambrian fossils which are represented in the fossil early to middle Cambrian (Terreneuvian and Cambrian Series 2 and 3) record by a multitude of small plate- or cone-shaped sclerites (Bengtson 1970; Landing 1984; Bengtson *et al.* 1990; Conway Morris and Chen 1990). Tommotiid sclerites typically exhibit co-marginal ribs representing basinal/marginal growth patterns. The sclerites are considered to be phosphatic by original composition (Balthasar *et al.* 2009). They typically occur in two or three distinct morphs united by identical surface sculptures and shell structures. Individual sclerite morphs may be bilaterally symmetrical, but most are asymmetrical and occur in sinistral and dextral symmetry variants. The co-occurrence of multiple sclerite morphs and symmetry variants suggest that the skeleton of most tommotiids was a complex, cataphract external scleritome.

In recent years, the discovery of partially articulated specimens of the tommotiids

1 *Eccentrotheca* Landing, Nowlan and Fletcher, 1980 and *Paterimitra* Laurie, 1986 has
2 revealed that the scleritome of at least some tommotiids was tubular, constructed by a series
3 of vertically stacked sclerite rings (Skovsted *et al.* 2008, 2009c, 2011; Larsson *et al.* in press).
4 Specialization of specific sclerites in the scleritome led to the evolution of a bivalved shell
5 and similarities in morphology, ornament and ultrastructure suggest that tommotiids form part
6 of the stem group of the lophophorate (i.e. Brachiopoda plus Phoronida) phyla (Skovsted *et*
7 *al.* 2008, 2009a, 2009c; Holmer *et al.* 2008b, 2011; Balthasar *et al.* 2009; Murdock *et al.*
8 2012; Larsson *et al.* in press).

9 Tannuolinids are a group of tommotiids united by a specific laminate shell structure
10 penetrated by externally open tubes believed to have been occupied in life by brachiopod-like
11 setae (Holmer *et al.* 2002; Ushatinskaya 2002; Williams and Holmer 2002; Li and Xiao
12 2004). Two tannuolinid genera have been described to date: *Tannuolina* Fonin and Smirnova,
13 1967 which is characterized by two sclerite types, narrowly compressed and usually
14 bilaterally symmetrical sellates and pyramidal, asymmetrical mitrals and *Micrina* Laurie,
15 1986 which combines similarly constructed sellate sclerites with a single bilaterally
16 symmetrical mitral sclerite. The larval shell morphology and the generally brachiopod-like
17 morphology of *Micrina* sclerites, with paired internal apophyses (teeth *sensu* Laurie 1986, see
18 Williams and Holmer 2002) in mitral sclerites and paired muscle scars and apparent
19 articulating surfaces in the sellate sclerites have led to a reconstruction of this tommotiid as a
20 fully bivalved animal and the most advanced tommotiid member of the brachiopod stem
21 group (Holmer *et al.* 2008b, 2011).

22 Tannuolinids have previously been known to occur in the Altai-Sayan Fold belt (Fonin
23 and Smirnova 1967), Australia (Bischoff 1976; Laurie 1986; Gravestock *et al.* 2001), China
24 (Qian and Bengtson 1989; Li and Xiao 2004), Mongolia (Esakova and Zhegallo 1996) and
25 Siberia (Kouchinsky *et al.* 2010). *Tannuolina* sp. has also been reported from the lower

Cambrian of Spain (Fernández-Remolar 2002). Herein we report the first occurrence of both *Tannuolina* and *Micrina* in the lower Cambrian of the Anti-Atlas Mountains of Morocco, in the case of *Micrina*, extending the known range into western Gondwana.

MATERIAL AND METHODS

Specimens of *Tannuolina maroccana* and *Micrina* sp. were derived from limestone samples from the lower Cambrian at Tazemmourt, Morocco. Samples were digested in dilute acetic acid and the resulting acid resistant residues were screened for fossils at the department of Earth Sciences of the Université de Lille 1. Selected tannuolinid specimens were coated with gold/palladium and studied using Scanning Electron Microscopy (SEM) at the Swedish Museum of Natural History.

GEOLOGICAL AND PALEOENVIRONMENTAL SETTING

In NW Africa, most of the Ediacaran-Cambrian successions are located in the High-Atlas and Anti-Atlas Mountains (Souss Bassin, Fig. 1; Geyer, 1989). In the Souss Bassin, the microbial community remains unaffected across the Ediacaran-Cambrian transition as preserved in the thick, otherwise poorly fossiliferous, Adoudou, Lie-de-Vin and Igoudine carbonate-dominated formations which represent a restricted, shallow-water environment. Immigration of typical early Cambrian metazoan shelly-fauna was delayed to the beginning of the Atdabanian, favored by an environmental shift to open-marine conditions recorded by a distinct facies change between the Igoudine and Amouslek formations (Álvaro *et al.*, 2006).

The Tazemmourt section (GPS coordinates 30°23'N/08°48'W of the Taroudannt map sheet; western Anti-Atlas), where the studied remains were recovered, was formerly part of the Souss Bassin (Fig. 1B). In this section (fully described by Álvaro *et al.*, 2006, see also Álvaro and Debrenne, 2010, Fig. 2), the Tiout Member of the Igoudine Formation is

dominated by stromatolitic reef and peloidal limestone strata deposited in peritidal and subtidal environments. Its uppermost part is characterized by prograding ooidal to oncoidal carbonate shoals and marks the shift to open marine conditions in an unstable tectono-sedimentary context. The top of the Tiout Member was formerly defined as a massive archaeocyathid bioherm which was later included in the following Amouslek Formation (Alvaro *et al.*, 2006). In the Tazemmourt section, the overlying Amouslek Formation is marked by massive immigration of shelly metazoans and represents large development of archaeocyathan-microbial reef and perireefal limestone sediments (Álvaro *et al.*, 2006). The Adtabanian (Cambrian Series 2, stage 3) age of the Tiout Member and Amouslek Formation is based on the occurrence of the oldest Moroccan trilobites at its base (*Eofallotaspis* trilobite Zone; Sdzuy, 1978; Geyer, 1989) and on archaeocyath zones (*Erismacocisnus fasciolus*–*Retecoscinus minutus* archaeocyathan Zone; Debrenne and Debrenne, 1995). The tommotiid remains described below occurred in the flanks of archaeocyathan-microbial patches and bioherms in association with cancelloriid sclerites, sponge spicules, hyoliths, and tube-shaped microfossils (hyolithelids, torellidellids), brachiopods and trilobites. At Tazemmourt, their occurrence is restricted to the lower 50 metres of the Amouslek Formation

SYSTEMATIC PALAEONTOLOGY (Skovsted and Clausen)

All figured specimens from Morocco are deposited in the Palaeozoology collections of the Swedish Museum of Natural History, Stockholm (acronym NRM). Illustrated specimen of *Eccentrotheca helenia* Skovsted *et al.*, 2011 from South Australia is deposited in the palaeontological collections of South Australian Museum, Adelaide (acronym SAMP). Illustrated specimens of *Micrina etheridgi* (Tate, 1892) are housed in Commonwealth Palaeontological Collections, Canberra (acronym CPC).

1

2 *Terminology*

3 The terminology deployed to describe the gross morphology of *Tannuolina* sclerites from
4 Morocco follows that of Bengtson (1970), Qian and Bengtson (1989) and Li and Xiao (2004).
5 See also Fig. 3. The sub-rectangular mitral sclerites of *Tannuolina* are divided into four sides,
6 the longer decrescent and acrescent sides and the shorter carinate and obcarinate sides. The
7 carinate side bears an internal ridge, the carinae. The compressed sellate sclerites have a
8 larger, convex sellate side and a shorter, concave duplicatural side with a triangular to oval
9 apertural opening. The duplicatural side is often fused with to the internal surface of the
10 sellate side, forming a duplicature. The sellate side may exhibit a depressed area, the sella.
11 The terminology used to describe *Micrina* sp. is developed from the terminology introduced
12 by Laurie (1986) and Williams and Holmer (2002). The cone-shaped mitral sclerites have a
13 blunt apex and a sub-circular aperture. The apex is eccentric and slightly overhangs the sub-
14 apical surface which in some species of *Micrina* is divided into deltoid and perideltoid areas
15 by narrow radiating folds. The sub-apical surface internally bears two ridge- or teeth like
16 extensions, the apophyses. The sellate sclerite of *Micrina* has not been found in *Micrina* sp.,
17 but in other species of the genus it is similar to symmetrical sellate sclerites of *Tannuolina*
18 with differentiated sellate and duplicatural sides.

19 The shell of tannuolinids is laminar and individual lamina may be separated by open
20 slits. The shell exhibits open pores on some or all external surfaces. The pores are openings of
21 tubular structures (primary tubes) that are mainly inserted parallel to shell laminae and may be
22 associated with a second set of pores (secondary tubes) that penetrate the laminar shell.

23

24

Stem BRACHIOPODA

25

Order TOMMOTIIDA Missarzhevsky, 1970

Family TANNUOLINIDAE Fonin and Smirnova, 1967

Genus TANNUOLINA Fonin and Smirnova, 1967

*1967 *Tannuolina* n. gen.; Fonin and Smirnova, p. 17.

1989 *Tannuolina* Fonin and Smirnova; Qian and Bengtson, p. 81.

1990 *Tannuolina* Fonin and Smirnova; Conway Morris and Chen, p. 177.

1996 *Tannuolina* Fonin and Smirnova; Esakova and Zhegallo, p. 113.

2002 *Tannuolina* Fonin and Smirnova; Fernández-Remolar, p. 43.

2004 *Tannuolina* Fonin and Smirnova; Li and Xiao, p. 909.

Type species. Tannuolina multifora Fonin and Smirnova, 1967 from the Altai-Sayan foldbelt, south-western Siberia.

Diagnosis (emended). Tommotiid with two fundamentally different sclerites; low, cone-shaped and asymmetrical mitral sclerites with a rectangular to oval aperture and high, compressed and bilaterally symmetrical or asymmetrical sellate sclerites. The sclerite surface bears co-marginal growth lines and externally open tubular perforations.

Differ from *Micrina* in the presence of asymmetrical mitral sclerites and differential distribution of tubular perforations on different parts of the sclerites. Differ from all other tommotiids in the presence of open tubular perforations on the external surface.

Species included. Type species, *T. zhangwentangi* Qian and Bengtson, 1989, *T. fonini* Esakova in Esakova and Zhegallo, 1996, *T. pavlovi* Kouchinsky *et al.*, 2010 and *T. maroccana* n. sp.

Discussion. *Tannuolina maroccana* n. sp. which is described below differs substantially from

all other species of *Tannuolina* in the presence of both symmetrical and asymmetrical sellate sclerites so the recognition of the latter type of sclerite in *Tannuolina* requires an emendation of the generic diagnosis. The strong similarities in shell ornament and ultrastructure between the mitral and bilaterally symmetrical sellate sclerites (which are closely comparable to their counterparts in other species of the genus) and the more problematic asymmetrical sellate sclerites strongly suggest that they belong to the scleritome of *Tannuolina*. This interpretation is also strengthened by the co-occurrence of the same set of sclerite types in collections of apparently conspecific *Tannuolina* from rocks of similar age in Spain (Fernández-Remolar 2002). According to our interpretation, the sellate sclerites of *T. maroccana* occur in two morphs; one bilaterally symmetrical and one asymmetrical, the latter occurring in both sinistral and dextral symmetry variants.

We note that morphological variation is generally large in *Tannuolina* and that individual sellate sclerites of most species can be at least slightly asymmetrical (see Fonin and Smirnova 1967, pl. 2, figs 8-9; Qian and Bengtson 1989, fig. 53C,D; Conway Morris and Chen 1990, fig. 12.1-2). However, in describing *T. pavlovi* from the basal Tommotian of Siberia, Kouchinsky et al (2010, fig. 6) reported a single, strongly compressed and asymmetrical sclerite. Kouchinsky *et al.* (2010) interpreted this specimen as an aberrant mitral sclerite but morphologically this specimen is more closely comparable to associated sellate sclerites, indicating that asymmetrical sellate sclerites were present also in the scleritome of *T. pavlovi*. The morphology of sellate sclerites of *Tannuolina fonini* from Mongolia is difficult to characterize based on available descriptions and illustrations, but appears to be asymmetrical (Esakova and Zhegallo 1996, fig. 29, pl. 6, figs 5, 6), although this is not specifically stated in the description (Esakova and Zhegallo 1996, p. 113). However, the sellate sclerites are described as having a marginal sella, a feature which is reminiscent of the asymmetrical sellate sclerites of *T. maroccana*. Until better illustrations of the Mongolian species are

available, detailed comparison of *T. fonini* with other species of the genus will be difficult.

As asymmetrical sellate sclerites have not been recognized in the type species, *Tannuolina multifora* from the Altai Sayan Foldbelt of south-western Siberia (Fonin and Smirnova 1967), an alternative approach to the systematic treatment of the new Moroccan species would be to propose a new genus to accommodate it. However, the type species was one of the first tomotiids ever described and has never been revised. Consequently, the possibility that other sclerite morphs are present also in the type species cannot be excluded at the present time, particularly after the recognition of such rare sclerites also in *T. pavlovi* and possibly in *T. fonini*. Based on the strong similarities in the morphology of the mitral sclerite, including the presence of a carina and details of the pattern of setigerous perforations, and the remaining uncertainties in the composition of the *Tannuolina* scleritome, we prefer a more conservative approach and choose to place the Moroccan species in *Tannuolina*. The interpretation that the sellate sclerites of *Tannuolina* may occur in both symmetrical and asymmetrical variants suggests that the scleritome structure of *Tannuolina* is more complicated than previously appreciated and predicts that such sclerites may be recognized in future investigation of *Tannuolina* from other parts of the world.

Tannuolina maroccana Skovsted and Clausen n. sp.

Figures 4-9

2002 *Tannuolina* sp. Fernández-Remolar; p. 44, pls 1-2.

Diagnosis. Species of *Tannuolina* characterized by the presence of both narrowly compressed, bilaterally symmetrical sellate sclerites and asymmetrical, openly coiled sellate sclerites with deep internal cavity, and a shallow sella and sub-central keel on the sellate side. Sellate

sclerites with open perforations concentrated to both lateral margins and to a narrow zone surrounding the lateral margin on both the duplicatural and sellate sides. Mitral sclerites with convex decrescent side, a shallow external furrow and a low internal carina on the carinate side and poorly differentiated obcarinate and acrescent sides. Obcarinate-acrescent sides with multiple, externally open perforations and decrescent side with a fine cancellate surface ornament. A single perforation, or a small group of large perforations are located close to boundary of the initial growth increment, at the junction of the decrescent and carinate sides.

Differ from all species of the genus in the presence of asymmetrical sellate sclerites with a deep cavity and the presence of a cancellate surface ornament on the decrescent side. Differ from *T. multifora* and *T. zhangwentangi* in the absence of sella and duplicature in sellate sclerites and in the more oval outline of mitral sclerites, from *T. multifora* in the absence of a transverse row of pores on the decrescent side, and from *T. zhangwentangi* in the higher concentration and larger maximum diameter of open pores along the lateral margins in sellate sclerites and on the obcarinate-acrescent side of mitral sclerites. Differ from *T. pavlovi* in the depressed profile and the presence of an external furrow and internal carinae in mitral sclerites and in the presence of open perforations in a zone on both sides of the lateral margins of sellate sclerites. Differ from *T. fonini* in the central keel and wide lateral sella of sellate sclerites.

Holotype. NRMX5267; Complete mitral sclerite from sample TZ-22, lower Amouslek Formation, Tazemmourt, Morocco.

Material. Three mitral sclerites preserving the apex (one sinistral, two dextral), one bilaterally symmetrical sellate sclerite and five asymmetrical sellate sclerites (two sinistral, three dextral)

as well as numerous shell fragments from the lower Amouslek Formation at Tazemmourt, Morocco.

Description. The mitral sclerite is low, conical with a blunt apex and is sub-rectangular to oval in outline (Fig. 4A-D). The maximum length is estimated to at least 6 mm, based on fragmentary specimens (Fig. 5). The decrescent and carinate sides are well developed and demarcated by narrow zones with distinct changes in surface sculpture while the obcarinate and acrescent sides are developed as a single, smoothly curved and strongly convex plate (Fig. 4A). The decrescent side is convex and gently arched in lateral view (Figs 4B, 5B). The carinate side has a shallow furrow running close to and parallel with the junction with the decrescent side and the furrow is internally associated with a low carina (Fig. 4D, E, H). The decrescent side is ornamented by regular co-marginal folds and in larger specimens a superimposed cancellate pattern formed by narrow, slightly undulating ridges (Figs 4A, 5C, D, G). The co-marginal ornament is more uneven on the carinate side and even more so on the obcarinate-acrescent side (Figs 4J, 5G, H). No traces of a cancellate surface sculpture have been identified on these parts of the sclerite. In smaller specimens the decrescent and carinate sides lack pores while the obcarinate-acrescent sides are covered by closely set pores (Fig. 4C, J). The pores are largest on the obcarinate end of the plate and get successively smaller and less numerous along the acrescent side towards the junction with the carinate side (Fig. 4A, I). The pore diameter increases with successive growth laminae until a maximum diameter of 80µm is attained. In larger specimens small pores are also present on the decrescent side, typically most numerous and of largest diameter close to the junction with the obcarinate side (Fig. 5A-D). The initial growth stage of the mitral sclerite mimics the general shape of the sclerite and bears occasional small pore openings (Fig. 4F). A single larger pore or a small group of pores are present at the margin of the initial shell, close to the junction of

1 the carinate and decrescent sides (Fig. 4G, K, M).

2 The bilaterally symmetrical sellate sclerite is represented in the material by a single
3 specimen, which unfortunately was lost after initial SEM investigation of the duplicatural side
4 (Fig. 6). The sclerite is a gently concavo-convex (duplicatural side concave) and strongly
5 compressed cone. However, the duplicatural side is not fused to the sellate side and the
6 sclerite remains an open cone and lacks a true duplicature. The duplicatural side is almost as
7 large as the sellate side and only a narrow aperture lacking muscle scars is exposed. Pores are
8 distributed along the lateral margins of the sclerite but the exact pattern is not observable.

9 The asymmetrical sellate sclerites are deep, openly coiled cones occurring in sinistral and
10 dextral symmetry variants (Fig. 7). The duplicatural side is flat or gently convex and shorter
11 than the sellate side (Fig. 7A, D, K). The apex is coiled and overhang the duplicatural side.
12 The sellate side of the sclerites is a wide, convex plate with a low, sub-central keel and a wide,
13 poorly expressed concave sella developed on the part of the sclerite which the apex is coiled
14 towards (Fig. 7B, F, G, I, J). The internal cavity is deep and wide but is partly constricted by
15 internally deflected shell laminae (Fig. 7A, E). The surface of the sclerite, on both sellate and
16 duplicatural sides, is covered by uneven co-marginal folds and well-preserved portions of
17 sclerites exhibit a superimposed cancellate pattern of fine ridges (Fig. 7M). Open pores are
18 present on all parts of the sclerite but are rare on the duplicatural side and on the sella. More
19 numerous pores are found on the sellate side lateral to the sella and central keel. The pores are
20 most strongly developed, and attain the largest diameter (up to 50µm), at the lateral margins
21 of the sclerites and along narrow zones adjacent to the lateral margins on both the sellate and
22 duplicatural sides (Fig. 7C, H, M). The initial part of the sclerite is not well preserved in any
23 specimen but open pores appear to be present along the lateral margins almost all the way to
24 the apex (Fig. 7C).

1 *Microstructure.* The shell of both sellate and mitral sclerites is composed of closely spaced
2 laminar sheets separated by narrow slits. Along the inner surface of the sclerite the laminae
3 are parallel to the shell wall but the inclination of each lamina eventually changes
4 dramatically (by about 50-70°) (Fig. 8A-C). Both the laminae and the slits between them
5 simultaneously expand dramatically in thickness. The result is a shell structure with an inner
6 thin and densely laminated shell structure and a thicker outer zone of discordantly overlapping
7 shell wedges (Fig. 8C). The external pores present on some parts of the sclerite surface
8 represent the openings of tubular structures that are inserted into the wedges between and
9 almost parallel to the shell laminae (Figs 8C, 9B, G). The majority of these primary tubes end
10 when they intersect shell laminae along the zone where these change growth direction (Figs
11 8C, 9G). However, some tubes may penetrate one or two shell laminae (Figs 8D, 9C). Pore
12 openings consequently only penetrate to the internal surface of sclerites in a narrow zone
13 along the growing margin of the sclerite (Fig. 8B). The internal surface of the tubes exhibits
14 fine, longitudinal striations about 500 nm wide (Fig. 9C).

15 A second set of tubular structures penetrates the shell roughly perpendicular to shell
16 lamination and the externally open pores (Figs 8G, 9I). The second set of tubes connects via a
17 circular or oval opening to the primary tubes, a short distance inside the pore opening (Figs
18 8H, I, 9H). The diameter of the secondary tubes represents approximately 20-40% of the
19 primary tube diameter and no traces of longitudinal striations can be observed. The secondary
20 tubes are inserted perpendicular to shell lamination and appear to penetrate multiple shell
21 laminae and can sometimes be observed as narrow columns connecting laminae in the inner,
22 laminar zone of the sclerite wall (Figs 8G 9I).

23
24 *Discussion.* The co-occurrence of *Tannuolina maroccana* with a mitral sclerite of *Micrina* sp.
25 (described below) opens the possibility that one of the sellate sclerites morphs described

above represent the sellate sclerite of *Micrina* sp. However, all sellate sclerites from Tazemmourt exhibit an identical shell ultrastructure which is different from the regularly columnar ultrastructure of *Micrina* sp. This strongly suggests that all sellate sclerites recovered represent different sclerite types of a single species, *T. maroccana*.

Fernández-Remolar (2002) described *Tannuolina* sp. from the Córdoba area of the Ossa-Morena Zone, southern Spain, and reported an assemblage almost exclusively composed of mitral sclerites. The specimens from Spain were invariably fragmentary but, based on similarities in general morphology and the presence of a cancellate surface ornament on some parts of the sclerites, the illustrated specimens are likely to be conspecific with *Tannuolina maroccana*. Fernández-Remolar interpreted all asymmetrical sclerites as mitrals but, as argued above, we interpret openly coiled asymmetrical sclerites as a variant of the sellate sclerite, and the majority of the specimens illustrated by Fernández-Remolar (2002) seem to concur with this model. However, some Spanish specimens appear to represent genuine mitral sclerites (Fernández-Remolar 2002, pl. 2, figs 6-8, 16-18) while at least one specimen appear to represent the symmetrical variant of the sellate sclerite (Fernández-Remolar 2002, pl. 1, figs 9,10). According to this reinterpretation, the ratio of mitral to symmetrical and asymmetrical sellate sclerites in the Spanish *Tannuolina* sclerites illustrated by Fernández-Remolar (2002) is similar to the observed pattern among *Tannuolina* specimens from Morocco.

Occurrence. Cambrian Series 2, Stage 3 (Atdabanian equivalent) of Morocco and the lower Ovetian of southern Spain.

Genus MICRINA Laurie, 1986

Micrina sp.

Figure 10

Material. A single mitral sclerite from sample TZ-22, NRMX 5282.

Description. Cone-shaped, bilaterally symmetrical mitral sclerite with sub-oval apertural outline, the margins of which appear to be determined mainly by mechanical fragmentation (Fig. 10A). The bluntly rounded apex is inclined slightly over a broadly flaring sub-apical field without defined deltoid and perideltoid areas (Fig.10A-C). The surface of the shell appears to be partly exfoliated but reveals a series of concentric, sub-circular growth lines. Growth appears to be quite regular in some portions of the shell and more irregular in other parts, in particular on the sub-apical field (Fig. 10A, C).

The internal surface is poorly preserved but the interior of the sub-apical field bears a pair of low ridges, radiating (angle of divergence 22°) from the central area of the sclerite towards the anterolateral margins of the sub-apical field (Fig. 10D). The partly exfoliated ridges consists of low, ribbon-like structures raised approximately $25\text{ }\mu\text{m}$ over the inner surface of the shell and contain a series of slightly undulating but more or less parallel, horizontal tubes (Fig. 10E, F) with circular cross-section (diameter about $10\mu\text{m}$).

Microstructure. The laminar shell structure is relatively well preserved, revealing three sets of tubular internal structures. Most obvious are two sets of large tubes that open to the external surface. One set of tubes are horizontally inserted between successive shell layers and these tubes (diameter $10\text{--}16\mu\text{m}$) are typically associated with a distinct cylindrical indentation in succeeding shell layers (Fig. 10G, H). Almost invariably, each horizontal tube is associated with a vertical tube of similar dimension inserted close to the mouth of the cylindrical indentation (Fig. 10E-G). The vertical tubes open onto parts of the internal surface, but only

1 where the innermost shell layers have been lost (Fig. 10D). In between the large tubular
2 structures, the laminar shell is penetrated by a host of closely set acrotretid-like columns
3 (diameter 2-7 μ m), visible on shell surface as small pores or domes (Fig. 10I, J) and
4 sometimes directly observable in cross-section (Fig. 10H).

5
6 *Discussion.* This single specimen differs from all other tommotiid specimens from Morocco
7 in the bilaterally symmetrical, open cone shape and the presence of paired internal ribs on the
8 sub-apical field. The regularly columnar shell structure is also different from that of
9 *Tannuolina maroccana*, testifying to the independent origin of the specimen. Although the
10 specimen is relatively poorly preserved, similarities in general morphology (open cone shape,
11 bilateral symmetry, setigerous tubes) with *Micrina* from Australia and South China (Laurie
12 1986; Ushatinskaya 2002; Williams and Holmer 2002; Li and Xiao 2004) suggest that this
13 specimen represents the mitral sclerite of a new species of *Micrina*. This identification is
14 supported by the presence of paired internal ridges on the sub-apical field, closely comparable
15 to the apophyses of the mitral sclerites in *Micrina* which may also contain parallel internal
16 tubes (Li and Xiao 2004). Externally the specimen differs from mitral sclerites of both the
17 known species of *Micrina*, *M. etheredgi* and *M. xiaotanensis* Li and Xiao, 2004 in the greater
18 length of the sub-apical field and the absence of a deltoid. The laminar shell structure is also
19 different from that of other species of *Micrina* by the lack of distal expansion of laminae and
20 the presence of acrotretid-like columns. However, *Micrina* from Australia and China are
21 exceptionally variable (Bischoff 1976; Laurie 1986; Li and Xiao 2004; CBS personal
22 observation) and consequently the single specimen from Morocco is left under open
23 nomenclature awaiting the discovery of additional material, preferably also including
24 specimens of the presumed sellate sclerite.

1 THE SCLERITOME OF *TANNUOLINA*

2 Despite the obvious problems of reconstructing a complex skeleton from disarticulated
3 elements, we present here one tentative reconstruction of *Tannuolina maroccana* (Fig. 11C,
4 D) which takes into account evidence from published records of fused *Tannuolina* sclerites,
5 relative sclerite proportions and comparisons to scleritome reconstructions of other
6 tomotiids.

7 Following the find of articulated specimens of the tomotiid *Eccentrotheca* exhibiting a
8 tubular scleritome composed of vertically stacked sclerite rings (Fig. 11A; Skovsted *et al.*
9 2008, 2011), the scleritome of *Micrina* was reinterpreted by Holmer *et al.* (2008b) as an open,
10 bivalved shell (Fig. 11B), closely comparable to that of brachiopods. The scleritome was,
11 according to the hypothesis presented (Holmer *et al.* 2008b), derived from the tubular
12 scleritome of *Eccentrotheca* by specialization of sclerites in the basal sclerite ring, coupled by
13 loss of subsequent sclerite rings. Holmer *et al.* (2008b) pointed out that *Tannuolina*, which
14 appears to be the tomotiid most closely related to *Micrina* based on the shared
15 microstructure and presence of setigerous tubes, must have had a more complicated
16 scleritome structure. Rare ontogenetically fused sclerites are known in *Tannuolina*
17 *zhangwentangi* from China (Qian and Bengtson 1989; Li and Xiao 2004), and these
18 specimens show that the asymmetrical mitral sclerites occurred in pairs, arranged along their
19 decrescent sides (Li and Xiao 2004, fig. 5.2-4,13) while the symmetrical sellate sclerites occur
20 in a longitudinal file, the sellate side of one sclerite fused with the duplicatural side of the
21 following sclerite (Qian and Bengtson 1989, fig. 55; Li and Xiao 2004, fig. 4.1,2). As noted
22 by Holmer *et al.* (2008b) the fused pair of mitral sclerites in *T. zhangwentangi* forms a
23 bilaterally symmetrical unit and is likely a functional equivalent of the single mitral sclerite in
24 *Micrina* with the combined carinate sides representing the deltoid of *Micrina* and the carinae
25 functionally equivalent of the apophyses in *Micrina*.

1 If the scleritome model proposed for *Micrina* is extended to *Tannuolina*, the presence of
 2 longitudinally fused sellate sclerites indicates that the scleritome of *Tannuolina* contained
 3 more than one sclerite ring. However, longitudinal repetition of the mitral sclerites would be
 4 unexpected if the carinae are functional equivalents of the apophyses in *Micrina*, as these
 5 structures are interpreted to function in the articulation of the mitral sclerite with the opposing
 6 sellate sclerite (Holmer *et al.* 2008b) and would have little meaning in subsequent sclerite
 7 rings. Despite the limited and fragmentary nature of the available material, we also note that
 8 in *T. maroccana*, the maximum size of the mitral sclerites appear to exceed that of the sellate
 9 sclerites. This pattern is observable also in other species of *Tannuolina*, in particular if the
 10 apertural area of the high and narrow sellate sclerites is compared to the extended aperture of
 11 the mitrals (and thus the area of the soft parts directly covered by the sclerites). When
 12 arranged on opposing sides of a tube, multiple and partly overlapping sellate sclerites
 13 arranged in a longitudinal file would be required to cover the same surface area as a single
 14 pair of transversely arranged mitral sclerites.

15 In our reconstruction of the scleritome of *Tannuolina maroccana* (Fig. 11C, D) a single
 16 pair of mitral sclerites, arranged with their decrescent sides facing each other and with the
 17 carinate sides facing the base of the scleritome, cover one lateral half of the tubular scleritome
 18 (Fig. 11C). The opposing half of the scleritome consists of a longitudinal row of partly
 19 overlapping sellate sclerites arranged, in accordance with the model proposed for *Micrina* and
 20 the record of fused sellates in *T. zhangwentangi*, with apices facing downwards and the
 21 duplicatural sides towards the mitral sclerites (Fig. 11D). The presence of both symmetrical
 22 and asymmetrical sellate sclerites is represented in the reconstruction by the incorporation of a
 23 single symmetrical sellate sclerite at the base of the scleritome (directly opposing the
 24 combined carinate sides of the mitral sclerites) while subsequent sclerite rows consist of pairs
 25 of dextral and sinistral asymmetrical sellate sclerites arranged with proximal lateral edges

facing each other. The absolute number of sellate sclerite rows and the number of rows with symmetrical *versus* asymmetrical sellates is conjectural (and could be influenced by ontogenetic variation), although the model presented here roughly corresponds to the sclerite proportion in our material.

The proposed model could easily be expanded to other species of *Tannuolina* by modifying the number and nature of sellate sclerite rows. The model predicts that sellate sclerites should be more numerous than mitral sclerites and the model could possibly be tested by analysis of large and well-preserved collections. Most of the hitherto described collections of *Tannuolina* are relatively small (N<100 specimens), but at least in the best known species, such as *T. zhangwentangi* from China, the majority of reported specimens are sellates (Qian and Bengtson 1989: N= 55, 64% sellates; Li and Xiao 2004: N= 64, 61% sellates; Conway Morris and Chen never reported the sclerite ratio in their collections). However, a majority of mitral sclerites was recently reported for *T. pavlovi* from Siberia (Kouchinsky *et al.* 2010: N=25, 40% sellates), and approximately equal numbers of sellates and mitral sclerites were reported for *T. fonini* from Mongolia by Esakova and Zhegallo (1996; N=25, 52% sellates). The original description of the type species (*T. multifora*) from the Altai-Sayan Foldbelt, was based on 3800 specimens (Fonin and Smirnova 1967), but unfortunately, no information on the relative abundance of sellate and mitral sclerites was given by the authors. The applicability of relative sclerite proportions in scleritome analysis may be limited as sclerite ratios are likely to be heavily influenced by pre-deposition sorting and other taphonomic factors. In *Micrina etheredgi* (Tate, 1892) from South Australia (the currently best known tannuolinid), the ratio of mitral and sellate sclerites has been shown to vary extensively (by more than a factor 200) between collections (Holmer *et al.* 2008b).

TANNUOLINID EVOLUTION

1 The oldest known tannuolinid is *Tannuolina pavlovi* from the basal Tommotian Stage of
2 Siberia (Kouchinsky *et al.* 2010). This species is represented by asymmetrical mitral sclerites
3 and narrowly compressed symmetrical sellate sclerites with an open internal cavity but
4 without a sella. As discussed above, Kouchinsky *et al.* (2010, fig. 6) also illustrated a
5 narrowly compressed and asymmetrical specimen, interpreted by them as an aberrant mitral
6 sclerite but herein reinterpreted as an asymmetrical sellate sclerite. However, the total number
7 of reasonably complete specimens available (Kouchinsky *et al.* 2010) was low and the
8 association in Morocco of similar asymmetrical specimens with specimens of more
9 conventional morphology suggests that the scleritome of *Tannuolina* was more complex than
10 originally thought. However, if *Tannuolina* evolved from a tommotiid with a complex tubular
11 scleritome like that of *Eccentrotheca* (Homer *et al.* 2008b), the presence of asymmetrical
12 sclerites of both types in the scleritome is not unexpected.

13 The occurrence of *Eccentrotheca* in southeastern Newfoundland (Member 4 of the
14 Chapel Island Formation; late Fortunian; Landing *et al.* 1989; Kouchinsky *et al.* 2012)
15 predates all other eccentrothecimorph (including tannuolinid) tommotiids except the
16 problematic *Porcauricula* Qian and Bengtson, 1989 (late Fortunian; Kouchinsky *et al.* 2012).
17 No bilaterally symmetrical sclerites are present in the scleritome of *Eccentrotheca* and the
18 sclerite morphology is highly variable, with each sclerite apparently individually adapted to
19 the margins of adjacent sclerites (Skovsted *et al.* 2011). The compressed sellate sclerites of
20 tannuolinids could conceivably be derived from the morphologically similar, high and
21 laterally compressed sclerites of *Eccentrotheca*, and these are always asymmetrical (most
22 specimens exhibit a distinct apical twist; Skovsted *et al.* 2011). Bilateral symmetry of sellate
23 sclerites in *Tannuolina* thus appears to be a secondary adaptation. The mitral sclerites of
24 tannuolinids are more easily compared to the low, cap-shaped sclerites of *Eccentrotheca* but
25 the lack of persistent morphological characteristics in the latter precludes a detailed analysis

of the potential homology of these sclerites.

If the presence of asymmetrical sellate sclerites in *Tannuolina pavlovi* and *T. maroccana* is considered to be primitive, the apparent absence of asymmetrical sellate sclerites in most species of *Tannuolina* suggests a general tendency to replace asymmetrical sclerite pairs with symmetrical sclerites. If expanded to the mitral sclerites and combined with a reduction in sellate sclerite number, this tendency would essentially result in the evolution of a bivalved scleritome like that proposed for *Micrina* (Holmer *et al.* 2008b). The fossil record of tannuolinids may thus provide a record of the stepwise evolution of the bivalved brachiopod bodyplan from a multi-component, tubular origin.

SETIGEROUS SHELL STRUCTURES

Similarities between the perforate shell structure of tannuolinid tomotiids and many Cambrian brachiopod-like fossils have been a focal point of studies on the origin of brachiopods for the last decade (Holmer *et al.* 2002; Ushatinskaya 2002; Williams and Holmer 2002) and it has been convincingly argued that many of these structures originally housed shell penetrating setae similar to follicular setae of modern brachiopods (Williams and Holmer 2002). Such structures have since been identified in a number of Cambrian and Ordovician phosphatic brachiopods and stem group brachiopods (Holmer *et al.* 2008a) as well as in some Ordovician calcareous brachiopods (i.e. orthids; Jin *et al.* 2007). Although the tomotioid ancestry of the phylum Brachiopoda is now well established based on several lines of evidence, including articulated tomotiids (Skovsted *et al.* 2008, 2009c, 2011; Larsson *et al.* in press), shell ultrastructure (Balthasar *et al.* 2009) and larval shell morphology (Holmer *et al.* 2011), the tendency to interpret all shell perforations of tomotioid sclerites and stem brachiopod shells as setigerous tubes needs a critical reevaluation.

The key feature of setigerous tubes in fossil brachiopods and stem group brachiopods

are the fine longitudinal striations of the internal surface of the tubes, which are commonly interpreted to reflect microvilli in the original setae (Holmer *et al.* 2002, 2008a; Williams and Holmer 2002). This interpretation was confirmed by the find *in situ* of phosphatized setae in Ordovician brachiopods from Anticosti Island (Jin *et al.* 2007). However, such striations are not present in all types of perforations that have been interpreted as setigerous tubes (Skovsted and Holmer 2003; Balthasar 2004; Holmer *et al.* 2008a). The configuration of tubular perforations in *Micrina* and *Tannuolina* from Morocco suggests that although some tubular perforations in stem brachiopods housed setae, other perforations were formed in a different way.

Relation of tubes in Micrina and Tannuolina

It has already been noted that several sets of interconnected tubes occur in tannuolinids (Williams and Holmer 2002; Holmer *et al.* 2008a; Kouchinsky *et al.* 2010) and this is evidently the case in both *Micrina* and *Tannuolina* from Morocco. In *Micrina* sp. the location of vertical and horizontal perforations are clearly correlated, with one vertical opening associated with each horizontal tube. The location of the vertical openings at, or close to, what was probably the external opening of the horizontal tubes appears to preclude the possibility that both sets of tubes contained setae. Unfortunately, exfoliation of this specimen does not allow the preservation of longitudinal striations but the tubular depressions in succeeding shell layers associated with the horizontally inserted tubes suggest that these originally housed setae. Consequently, the vertical tubes were probably formed in a different way and are unlikely to have housed setae. This interpretation is strengthened by the preservation of the vertical tubes, which appear to be constructed by annular rings and to lack a well-defined inner wall. In some cases smaller acrotretid-like columnar structures of the normal shell structure are incorporated into the wall of the vertical tubes (Fig. 10I). This pattern is

presumably a reflection of differential phosphatization of shell laminae in a zone around the vertical perforation.

Tannuolina maroccana exhibits what appears to be numerous vertically inserted and internally striated tubes on the obcarinate-acrescent side of the mitral sclerite and along the lateral margins of the sellate sclerites (as well as intermittently on other parts of the sclerites). The second set of tubular structures in *T. maroccana* opens directly into the striated primary tubes, close to their external opening and are inserted more or less perpendicular to these tubes. This configuration may appear to differ dramatically from the structure of *Micrina* sp., but when the outward bend and distal expansion of shell laminae in *T. maroccana* is taken into account, it is apparent that the primary tubes are actually inserted parallel to shell lamination and the secondary tubes perpendicular to lamination. The primary tubes of *T. maroccana* are thus homologous to the horizontal tubes of *Micrina* sp., while the secondary tubes are homologous to the vertical tubes of *Micrina* sp.

Micrina etheridgei from Australia represents a similar case where the tubes may sometimes be vertically inserted in relation to the shell surface, but still parallel to shell lamination when the outward bend and distal expansion of laminae is taken into account (Williams and Holmer 2002; Balthasar *et al.* 2009, supplementary fig. 1). Secondary tubes inserted perpendicular to the striated tubes and associated with the mouth of these larger tubes have also been observed in *M. etheridgei* (Williams and Holmer 2002, pl. 3, figs 2, 3; Holmer *et al.* 2008a, fig. 1A).

Shell penetrating tubes in brachiopods and stem brachiopods

Holmer *et al.* (2008a, p. 4) differentiated the secondary tubes of *Micrina* and the vertical tubes present in several different problematic Cambrian and Ordovician brachiopods as a unique type of shell structure, the so-called '*Micrina-Mickwitzia* columnar structure', and suggested

that these columns were, at least in some taxa, externally open tubes housing setae. The comparison to the problematic Cambrian brachiopod *Mickwitzia* Schmidt, 1888 was mainly based on the shell structure of '*Mickwitzia* cf. *occidens*', described from the lower Cambrian of Greenland by Skovsted and Holmer (2003). However, this species differs dramatically in both morphology and shell structure from *Mickwitzia*, and was later referred to a new genus, *Setatella* Skovsted *et al.*, 2010. Vertical tubes are present also in *Mickwitzia*, but these differ from those of *Setatella* and *Micrina* in the larger size and in deflecting laminar growth downwards into internally projecting cones (Balthasar 2004; Skovsted *et al.* 2009b). However, at least in one species, *Mickwitzia occidens* Walcott, 1908 from Nevada, horizontal tubes with internal striations are also present (Holmer and Popov 2007).

The shell structure of *Setatella significans* Skovsted *et al.*, 2010 from the lower Cambrian of Greenland and Labrador (i.e. *Mickwitzia* cf. *occidens sensu* Skovsted and Holmer 2003) is closely comparable to that of *Micrina* sp. from Morocco, with two sets of tubular perforations in addition to acrotretid-like columns (Skovsted and Holmer 2003; Skovsted *et al.* 2010). In *Setatella*, which probably belongs to the stem group of linguliform brachiopods, one set of tubes opens to the exterior and is inserted parallel to shell lamination, but these are only found on the pseudointerarea of the ventral valve. The horizontal tubes show longitudinal striations and cylindrical deformations of succeeding shell laminae that strongly suggest that they were originally occupied by setae (Skovsted and Holmer 2003, figs 10B1-B5, 12B1-B4). A second set of vertical tubes are present in other parts of the shell but these appear not to penetrate the primary shell and lack evidence of longitudinal striations (Skovsted and Holmer 2003, figs 8, 9). The preservation of the vertical tubes in *Setatella* from Greenland is also closely comparable to that of the vertical tubes in *Micrina* sp. from Morocco, being more akin to a vertical zone of phosphatization than a tube with a solid, mineralized inner wall (compare Fig. 10H, I with Skovsted and Holmer 2003, figs 11A, C,

12A).

As argued above, *Micrina*, *Tannuolina* and *Setatella* exhibit two fundamentally different sets of hollow tubes and it is probably more relevant to differentiate between setigerous tubes (externally open, internally striated, inserted parallel to lamination) and non-setigerous shell penetrating tubes (externally closed or connected to setigerous tubes, orthogonal to lamination, lack of striation) of the shell structure. Among the problematic Cambrian and Ordovician organophosphatic brachiopods with tubular shell structures discussed by Holmer *et al.* (2008a), confirmed setigerous tubes are present in tannuolinids, *Mickwitzia*, and on the ventral pseudointerarea of *Setatella*, but similar tubes inserted parallel to lamination have also been identified in the paterinid *Askepasma* Laurie, 1986 and possibly also *Heliomedusa* Sun and Hou, 1987 (Holmer and Popov 2007) and in the problematic *Estoniadiacus* Peel, 2003. Non-setigerous shell penetrating tubes are ubiquitous in tannuolinids, *Mickwitzia* and *Setatella* but similar tubes have been documented from the paterinid *Cryptotreta? undosa* as well as the problematic Ordovician genus *Bistramia* (Holmer *et al.* 2008a).

Function of the non-setigerous tubes in tommotiids

The nature and function of the non-setigerous tubes remain problematic, but the direct association of setigerous and non-setigerous tubes in *Tannuolina* and *Micrina* suggests that their functions were interconnected. In *Tannuolina* the non-setigerous tubes originate on the side of the setigerous tube facing the growing margin of the sclerite. The movement of follicular setae of modern linguliforms is controlled by a set of muscles connecting the follicle with the shell edge (Blochmann 1900), which means that the insertion point in the follicle is facing away from the growing margin of the shell. Consequently, there are no obvious structures in modern linguliforms that can be compared to the non-setigerous tubes of tannuolinids.

As the tannuolinid shell grew, the setae in the setigerous tubes are eventually isolated from the internal cavity by the formation of new shell laminae but the orthogonal inclination of the non-setigerous tubes means that these tubes could form a connection between the setae and the living tissue close to the shell margin. It is thus possible that the setae, rather than being lost or rendered redundant as the shell grew, continued to fill a sensory function throughout the life of the organism. The association of orthogonal and setigerous tubes remained in some of the earliest possible linguliforms (i.e. *Mickwitzia* and *Heliomedusa*), but appears to have been subsequently lost. However, the orthogonal tubes appear to have persisted in some lineages, even after the loss of setigerous tubes (i.e. *Setatella* and *Bistramia*).

CONCLUSIONS

- At Tazemmourt in the western Anti-Atlas Mountains of Morocco the lower Amouslek Formation has yielded a low diversity fauna of Small Shelly Fossils including two co-occurring tannuolinid tommotiids, *Tannuolina maroccana* n. sp. and *Micrina* sp.
- *Tannuolina maroccana* differs from other species of the genus in morphological details such as ornament and the pattern formed by externally open tubes in addition to a unique configuration of sclerite types. *Tannuolina maroccana* exhibits asymmetrical mitral sclerites comparable to those of other species of *Tannuolina* as well as two different types of sellate sclerites, one bilaterally symmetrical and one asymmetrical form occurring in sinistral and dextral symmetry variants.
- The scleritome of *Tannuolina maroccana* is tentatively reconstructed based on available information on sclerite morphology, relative sclerite proportions and evidence from naturally fused sclerites in the related *T. zhangwentangi* from South China. The reconstruction is based on the bivalved model proposed Holmer *et al.*

(2008a) for *Micrina etheridgei* as well as fused tubular sclerite composites of the more primitive tommotiid *Eccentrotheca*.

- In our reconstruction of *Tannuolina maroccana* a bilaterally symmetrical pair of mitral sclerites covers one lateral half of a short tubular scleritome while the opposing side is covered by a single symmetrical sellate sclerite at the base of the scleritome, followed by two rows of asymmetrical sellate sclerites occurring in bilaterally symmetrical pairs. The sellate sclerites are arranged with apices facing the base of the scleritome and subsequent rows are partly overlapping. The base of the scleritome is assumed to have housed an organic attachment organ and the top of the scleritome an opening and organs for filter-feeding.
- *Tannuolina maroccana* is thought to represent an intermediate stage in the evolution of the bivalved bodyplan of brachiopods from a multi-component, tubular tommotiid similar to *Eccentrotheca* via successive stages of specialization and sclerite loss. The addition of bilateral symmetry in tommotiids was a stepwise process and different species of *Tannuolina* can be thought to represent different stages in this process with asymmetrical sclerites occurring in pairs representing an ancestral pattern and being replaced by bilaterally symmetrical sclerite morphs in more advanced forms.
- Two fundamentally different types of tubular structures exist in the shell of tannuolinid tommotiids and in some Cambrian and Ordovician brachiopods. One type of tubular structure exhibits externally open pores and internal striation and presumably represents setae incorporated into the shell during growth of the organism. These tubes are almost invariably inserted parallel to shell lamination and rarely penetrate shell laminae. A second type of tubular structure lacking externally open pores and internal striations appear to penetrate shell laminae more or less orthogonally. No evidence exist that these tubes ever housed setae.

- In *Tannuolina maroccana* and *Micrina* sp. from Morocco the secondary tubes are directly connected to the setigerous primary tubes and appear to form a connection between the setae incorporated into the shell and the growing margin of the shell and thus a connection between the otherwise isolated setae and the living tissue of these organisms.
- The shell structure of *Micrina* sp. is remarkably similar to that of the stem group linguliform *Setatella* from Greenland and Labrador with primary and secondary tubes combined with an acrotretid-like columnar shell structure. However in *Setatella* the primary, setigerous tubes are restricted to the ventral interarea while secondary tubes are found all over the shell. This pattern suggests that problematic orthogonal tubes found in many early brachiopods may be relic structures similar to secondary tubes, persisting even after the evolutionary loss of the setigerous tubes that they were connected to in the ancestral tommotiids.

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Figure Captions

Fig. 1.- Geological sketches of (A) the High Atlas and Anti-Atlas Mountains, Morocco (after Geyer and Landing, 1995), and (B) the studied section (modified from Boudda *et al.*, 1979).

Fig. 2. Simplified stratigraphic section of the Igoudine-Amouslek transition measured in Tazemmourt (after Álvaro *et al.* 2006) and location of samples from which tommotiid remains were recovered; chrono-, bio- and litho-stratigraphic information based on Geyer *et al.*, (1995), Debrenne & Debrenne (1995) and Álvaro *et al.* (2006).

Fig. 3. Terminology used to describe *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at Tazemmourt, Morocco, sample TZ-22. A, Mitral sclerite, holotype NRMX 5267, external (apical) view; with decrescent, obcarinate, acrescent and carinate sides indicated as well as the position of the furrow on the carinate side. B, C, Sellate sclerite NRMX 5276. B, duplicatural side with the position of the duplicature and apertural opening indicated. C, sellate side with the position of the lateral sella, central keel indicated as well as the position of the proximal and distal edges.

Fig. 4. Mitral sclerites of *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at Tazemmourt, Morocco, sample TZ-22. A-H, holotype NRMX 5267. A, apical view of dextral sclerite. B, view from decrescent side showing dorsally arched sclerite margin. C, obcarinate side. D, carinate side. E, internal view showing position of carina. F, external detail of apex with outline of initial growth increment with multiple small pore openings and a single large opening at the junction of the carinate and decrescent sides. G, oblique view of apex from the

carinate side showing position of initial growth increment and large pore opening at the junction of the carinate and decrescent sides. H, detail of internal surface with the carina. I-K, NRMX 5268. I, apical view of broken sinistral sclerite. J, oblique view of junction between decrescent and obcarinate-acrescent sides. K, detail of apex with a group of three pore openings close to the junction of the (missing) carinate and decrescent sides. L, M, NRMX 5269. L, apical view of broken sinistral sclerite. M, detail of apex with a group of three pore openings close to the junction of the (missing) carinate and decrescent sides. Scale bars in A-E, I-J, L equal 500 μm , H, K, M equal 250 μm , F, G equal 50 μm .

Fig. 5. Mitral sclerites of *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at Tazemmourt, Morocco, sample TZ-22. A-D, NRMX 5270. A, external view of fragmentary specimen preserving parts of decrescent and carinate sides. B, lateral view from decrescent side showing curved apertural margin. C, detail of decrescent side close to presumed junction with obcarinate side showing reticulate surface ornament and clusters of small pores. D, detail of middle portion of decrescent side showing reticulate ornament and scattered pore openings. E-G, NRMX 5271 (see also Fig. 8D-J). E, external view of fragmentary specimen preserving parts of decrescent and obcarinate sides. F, lateral view of the obcarinate side. G, detail of junction between obcarinate and decrescent sides with contrasting reticulate ornament (decrescent side) and uneven growth increments perforated by vertical pores (obcarinate side). H, NRMX 5272 (see also Fig. 9G-I), external view of fragmentary specimen showing junction between obcarinate and decrescent sides. I, J, NRMX 5273. I, external view of fragmentary obcarinate/acrescent side with multiple growth increments permeated by vertical pore openings. J, detail of obcarinate/acrescent side showing distribution of pore openings. Scale bars in A, B, E, F, H, I equal 1 mm, C, D, G equal 500 μm , J equal 250 μm .

Fig. 6. Symmetrical sellate sclerite of *Tannuolina maroccana* n. sp., NRMX 5274 from Cambrian Series 2, stage 3 at Tazemmourt, Morocco, sample TZ-22. A, duplicatural view. B, apertural view showing open internal cavity. C, oblique lateral view of duplicatural side showing open perforations along lateral margin. Scale bars equal 500 μm .

Fig. 7. Asymmetrical sellate sclerites of *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at Tazemmourt, Morocco. A-C, NRMX 5275, dextral sclerite. A, oblique apertural view of duplicatural side showing coiled apex and deep and wide internal cavity, partly constricted by internally deflected shell laminae. B, sellate side with uneven growth increments, central keel and lateral sella. C, detail of apex and duplicatural side showing concentration of pores along the lateral margins of the sclerite. D-H, NRMX 5276, sinistral sclerite. D, duplicatural side showing eccentric position of coiled apex. E, sellate side showing central keel and lateral position of sella. F, oblique apertural view of duplicatural side showing partial constriction of internal cavity by deflected shell laminae. G, oblique apical view showing central keel, gently concave sella and flat lateral plate. H, oblique lateral view from distal edge showing concentration of open pores along the edge. I, J, NRMX 5277, fragmentary sinistral sclerite, sample TZ-10. I, sellate side showing central keel and proximal edge defining concave sella. J, oblique “apical” view showing concave sella. K-M, NRMX 5278, fragmentary sinistral sclerite. K, duplicatural view showing wide and deep partially constricted internal cavity. L, sellate side showing central keel and partially preserved sella. M, detail of distal edge in oblique apical view showing concentration of large open pores along the edge. All specimens except I, J from sample TZ-22. Scale bars in C, M equal 250 μm , all others equal 500 μm .

Fig. 8. Shell structure of *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at

1 Tazemmourt, Morocco, sample TZ-22. A-C, NRMX 5279, fragmentary dextral mitral sclerite.
 2 A, oblique view of obcarinate side. B, detail of fracture through obcarinate side showing
 3 laminae and multiple primary tubes. C, detail of primary tube with internal striations. D-J,
 4 NRMX 5271 (see also Fig. 5E-G), fragmentary mitral sclerite. D, oblique view of junction
 5 between decrescent and obcarinate sides. E, “apical” view exposing fracture surface through
 6 the shell. F, detail of apertural margin of obcarinate side showing inclined insertion of primary
 7 tubes. G, detail of E showing five primary tubes inserted in void between successive shell
 8 laminae, observe blunt termination of tubes where they intersect the succeeding shell lamina.
 9 H, detail of E showing vertical secondary tube connecting closely spaced shell laminae in the
 10 inner shell. I, detail of E showing broken primary tube with internal striations and the opening
 11 of a vertically inclined secondary tube close to the external opening of the primary tube. J,
 12 detail of G showing broken primary tube parallel to shell laminae and two secondary tubes
 13 penetrating the laminae. Scale bars in A, D, E, F equal 500 μm ; B, C, G-J equal 50 μm .

15 **Fig. 9.** Shell structure of *Tannuolina maroccana* n. sp. from Cambrian Series 2, stage 3 at
 16 Tazemmourt, Morocco, sample TZ-22. A-D, NRMX 5280, fragmentary mitral(?) sclerite
 17 preserving internal shell surface and part of the apertural margin. A, oblique internal view. B,
 18 internal view showing open pores in a zone along the apertural margin. C, detail of transverse
 19 section through the shell showing internal lamination of three successive growth increments,
 20 distal expansion and outward deflection of shell laminae and the insertion of primary tubes
 21 parallel to lamination (pore openings and insertion angles indicated by white arrows). D,
 22 detail of fracture zone through shell showing transverse sections through multiple primary
 23 tubes close to the external shell surface (lower part of picture) and fewer and smaller primary
 24 tubes penetrating into successive shell laminae. E, F, NRMX 5281, fragmentary mitral(?)
 25 sclerite. E, external view showing distribution of open pores in successive growth increments.

F, detail of E with external surface missing showing transverse sections of primary tubes and vertical secondary tubes. G-I, NRMX 5272 (see also Fig. 5H). G, external view of fragmentary mitral sclerite; H, detail of obcarinate surface in oblique “apical” view showing multiple pore openings representing primary tubes. I, detail of H showing openings of secondary tubes in the primary tubes. Scale bars in A, B, G, E equal 500 μm ; C, D equal 250 μm ; F, H, I equal 50 μm

Fig. 10. Mitral sclerite of *Micrina* sp., NRMX 5282 from Cambrian Series 2, stage 3 at Tazemmourt, Morocco, sample TZ-22. A, apical view. B, right lateral view showing apex overhanging sub-apical field. C, view of sub-apical field. D, internal view showing two diverging ridges on the sub-apical field. E, detail of broken internal ridge. F, detail of partly broken internal ridge with internal canals. G, detail of external surface with openings of horizontally inserted tubes, cylindrical depressions associated with horizontal tubes and vertical tubes opening at the termination of the cylindrical depressions. H, detail of partly exfoliated external surface showing vertical tubes. I, detail of vertical tube in exfoliated shell portion showing ring-like phosphatization of shell laminae along the tube, incorporating acrotretid-like columns. J, detail of broken shell margin showing acrotretid-like columns in successive shell laminae. K, detail of internal shell surface showing small domes and pores representing acrotretid-like columns. L, detail of internal shell surface showing partially phosphatized internal pores of acrotretid-like columns. Scale bars in A-D equal 500 μm ; E-H equal 100 μm ; I-L equal 20 μm .

Fig. 11. Tommotiid scleritomes. A, B, *Eccentrotheca helenia* Skovsted *et al.* 2011, SAMP 42537 (modified from Skovsted *et al.* 2011, text-fig. 9), exceptionally preserved specimen exhibiting tubular scleritome construction, A and B two different lateral views. C,

1 D, *Micrina etheridgi* (Tate, 1892), artificially produced specimen with conjoined sellate, CPC
2 39703, and mitral, CPC 39704, sclerites (modified from Holmer *et al.* 2008b, fig. 2). C, lateral
3 view. D, apical view. E, F, scleritome reconstruction for *Tannuolina maroccana* n. sp. E,
4 sellate side showing three partially overlapping sclerite rows, three of which are composed of
5 asymmetrical sellate sclerites. F, mitral side showing two conjoined asymmetrical mitral
6 sclerites. Scale bars equal 500 μm .

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Figure 1

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