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Internal homeomorphy in some Lower Cretaceous brachiopod genera (Terebratellidina) from the Carpatho-Balkanides, Eastern Serbia

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Key words: Brachiopoda, Terebratellidinae, new genus, internal homeomorphy, Early Cretaceous, eastern Serbia, Carpatho-Balkanides

ABSTRACT

Terebratellidine brachiopods of the Lower Cretaceous were studied with regard to their external and internal morphology as well as to the shell microstructure. These studies revealed that the Upper Barremian species *Timacella timacensis* (Antula) with semi-ribbed shell and the Lower Aptian *Psilothyris tamarindus* (J. de C. Sowerby) with smooth shell have an identical internal structure. At the present state of knowledge no mesozoic terebratellidine brachiopods with this internal homeomorphy were known. Both species are found in Lower Cretaceous shallow-water limestones of the Carpatho-Balkanides of eastern Serbia. A new genus, *Timacella*, with *Waldheimia* (*Eudesia*) *timacensis* Antula as type species, is described.

ZUSAMMENFASSUNG

An terebratellidinen Brachiopoden der Unterkreide wurden Untersuchungen der Aussen- und Innenmorphologie, sowie der Schalen-Mikrostruktur durchgeführt. Diese ergaben, dass die oberbarremische *Timacella timacensis* (Antula) mit teilweise gerippter Schale und die unteraptische *Psilothyris tamarindus* (J. de C. Sowerby) mit glatter Schale eine identische Innenstruktur aufweisen. Bisher waren keine mesozoischen terebratellidine Brachiopoden mit dieser internen Homoeomorphie bekannt. Beide Spezies kommen in unterkretazischen Flachwasserkalken der Karpato-Balkaniden von Ostserbien vor. Eine neue Gattung, *Timacella*, mit *Waldheimia* (*Eudesia*) *timacensis* Antula als Typusart, wird beschrieben.

1. Introduction

Buckman (1895) introduced the term homeomorphy, frequently used in paleontological literature, while studying Jurassic brachiopods. More than one example of external similarity and even identity among brachiopods has been reported. Alméras & Moulan (1982), Lobacheva (1990a) and Sandy (*in* Stanley et al. 1994) mention examples of external similarity. Sandy (personal communication 2000) mentioned the following example of internal similarity between two Lower Cretaceous terebratulid genera. When Middlemiss (1981) erected the Lower Cretaceous genus *Costithyris* (junior objective synonym of *Glosseudesia* Lobacheva 1974), he commented that it would be referred to the genus *Sellithyris* "because of the close similarity of the internal structures" if not for the external ribbing. We have no knowledge of any reference to Mesozoic terebratellidine brachiopods that are unlike externally but resemble in internal structures. An example of internal homeomorphy is given in this work; the semi-ribbed shell of Upper Barremian *Timacella timacensis* (Antula 1903) and the smooth shell of Lower Aptian *Psilothyris tamarindus* (J. de C. Sowerby 1836) have identical internal morphologic features.

The brachiopods described in this paper come from two localities, Crnoljevica and Faca Vajali, in eastern Serbia, Carpatho-Balkanides (Fig. 1). Both localities belong to the Kučaj-Svrljig zone in the Geticum (= Srednja Gora in Bulgaria).

Timacella timacensis (Antula) comes from the Upper Barremian succession of Crnoljevica, Svrljig Mountains, consisting of bioclastic limestones, marly limestones, and clayey limestones. The fossil community associated with brachiopods is abundant and represented by benthic foraminifers, algae, bivalves, cephalopods, and echinoids (Antula 1903, Radulović 2000).

The second species described here, *Psilothyris tamarindus* (J. de C. Sowerby) was found in the Lower Aptian marly limestones of Faca Vajali, Kučaj Mountains. In addition to bra-

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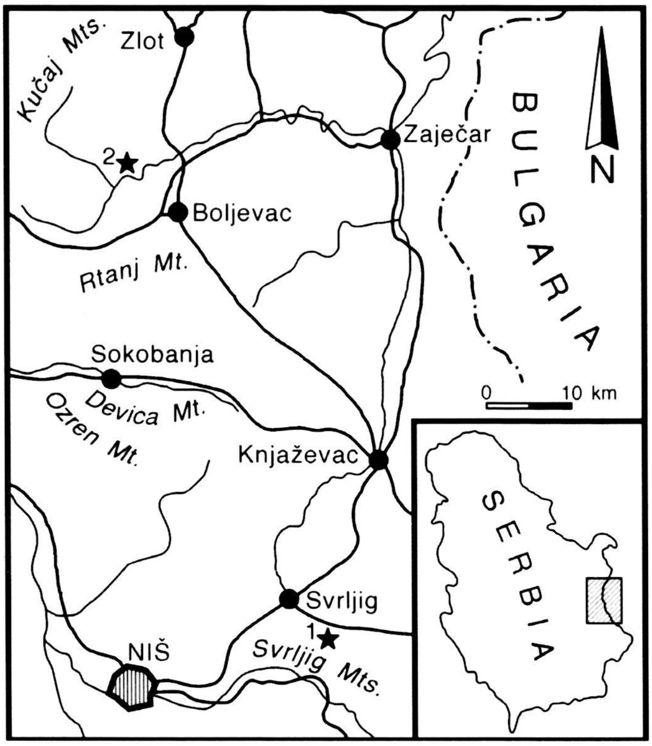

Fig. 1. Location map of the brachiopod localities (asterisk) in eastern Serbia, Carpatho-Balkanides. 1, Crnoljevica [(*Timacella timacensis* (Antula)]; 2, Faca Vajali [(*Psilothyris tamarindus* (J. de C. Sowerby)].

chiopods, the diverse marine fauna includes benthic foraminifers, algae, corals, gastropods, bivalves, and echinoids (Maran 1998).

The specimens are deposited in the collection of the Institute of Regional Geology and Paleontology, Faculty of Mining and Geology, University of Belgrade (number prefix RGF VR).

2. Systematic Palaeontology

Order Terebratulida Waagen 1883
Suborder Terebratellidina Muir-Wood 1955
Superfamily Dallinoidea Beecher 1893
Family Dallinidae Beecher 1893
Subfamily Dallininae Beecher 1893

Genus *Psilothyris* Cooper 1955

Type species. Psilothyris occidentalis Cooper 1955, Albian, Bisbee Quadrangle, Cochise County, Arizona.

Diagnosis (revised by Sandy 1986b). Smooth biconvex shell of medium size, circular to elongate oval to pentagonal outline. Beak suberect to erect with sharp beak ridges. Foramen circular, mesothyrid. Anterior commissure rectimarginate, uniplicate to ligate. Deltidial plates conjunct or disjunct. Dental lamellae subparallel. Outer hinge plates subhorizontal to dorsally inclined. Crural bases massive and triangular. Inner hinge plates anteriorly arched and fused. Crural processes converge ventrally. Loop long and thin, dalliniform with thickened descending branches and a broad transverse band. Median septum low, from 0.4 to 0.6 of valve length.

Distribution. Psilothyris is a widespread genus in the Aptian and Albian of England, France, Spain, Arizona, Mexico, Patagonia, Romania, Serbia, and possibly northern Africa and the Caucasus too. According to Sandy (1986b) and Sulser (1999) its occurrence in Berriasian, Lower Hauterivian and Barremian is doubtful.

Psilothyris tamarindus (J. de C. Sowerby 1836)
Pl. 1, Fig. 1–3; Pl. 2, Fig. 1–6; Fig. 2–4

1836 *Terebratula tamarindus* J. de C. Sowerby: 338, pl. 14, fig. 8
1867 *Terebratula tamarindus* J. Sowerby; Pictet: 105, pl. 26, fig. 1, 2
1872 *Terebratula* (*Waldheimia*) *tamarindus* J. Sowerby; Pictet: 96, pl. 204, fig. 1–3
1911 *Zeilleria tamarindus* d'Orb.; Petković: 7
1930 *Waldheimia* (*Zeilleria*) *tamarindus* Sow.; Petković: 107, pl. 2, fig. 8
1953 *Waldheimia* (*Eudesia*) *tamarindus* d'Orb.; Sučić: 111, pl. 3, fig. 11
1955 *Psilothyris tamarinda* (Sowerby); Cooper: 14, pl. 3C, fig. 25
1965 *Tamarella tamarindus* (J. de C. Sowerby); Owen: 57, pl. 1, fig. 2a–c, 8a–c, 10a–c; pl. 3, fig. 5a–c, 6a–c
1975 *Tamarella tamarindus* (J. de C. Sowerby); Calzada: 48, pl. 5, fig. 22
1975 *Tamarella tamarindus* (J. de C. Sowerby); Dieni & Owen *in* Dieni et al.: 200, pl. 38, fig. 7 (see for extensive synonymy)
1975 *Tamarella ramarindus* (Sowerby); Bârbulescu et al.: 128, pl. 4,fig. 1, 2, 4, 7
1978 *Waldheimia* (*Eudesia*) *tamarindus* Sow.; Jankićević: 119, 124, 129, 155
1979/80 *Waldheimia* (*Eudesia*) *tamarindus* Sow.; Jankićević: 225
1986a *Psilothyris tamarindus* (J. de C. Sowerby); Sandy: 191
1986b *Terebratula tamarindus* J. de C. Sowerby; Sandy: 146
1990 *Psilothyris tamarindus* (Sowerby); Smirnova: 113, pl. 32, fig. 5
1990b *Psilothyris tamarindus* (Sowerby); Lobacheva: 206
1999 *Tamarella tamarindus* (J. de C. Sowerby); Sulser: 226
1999 *Tamarella tamarindus* (Sowerby); Gaspard: 315, 319, 322, 324, pl. 2, fig. 9, 10

Nomenclative note. Although according to the rules of nomenclature (Art. 32d) *P. tamarindus* should be corrected to *P. tamarinda* because *Psilothyris* is feminine, we have kept the name *tamarindus*, as we didn't want to change the widely accepted name of the species. The same view is hold by Sulser and Manceñido (personal communication 2002).

Material. Nine complete specimens.

Description. External morphology. Shell of medium size, up to 17.6 mm long, with rounded pentagonal outline, equally moderately biconvex. Length usually greater than width. The maximum width at midlength; maximum thickness in the middle. Beak erect, low and wide with small circular mesothyrid foramen. Sharp beak ridges border wide and concave interarea. Rounded fold and shallow sulcus developed on the anterior quarter. Anterior commissure uniplicate. Median septum from 0.40 to 0.43 of the dorsal valve length.

Internal morphology. Two specimens have been sectioned (Fig. 2, 3). The internal characters as described for the *Timacella timacensis*.

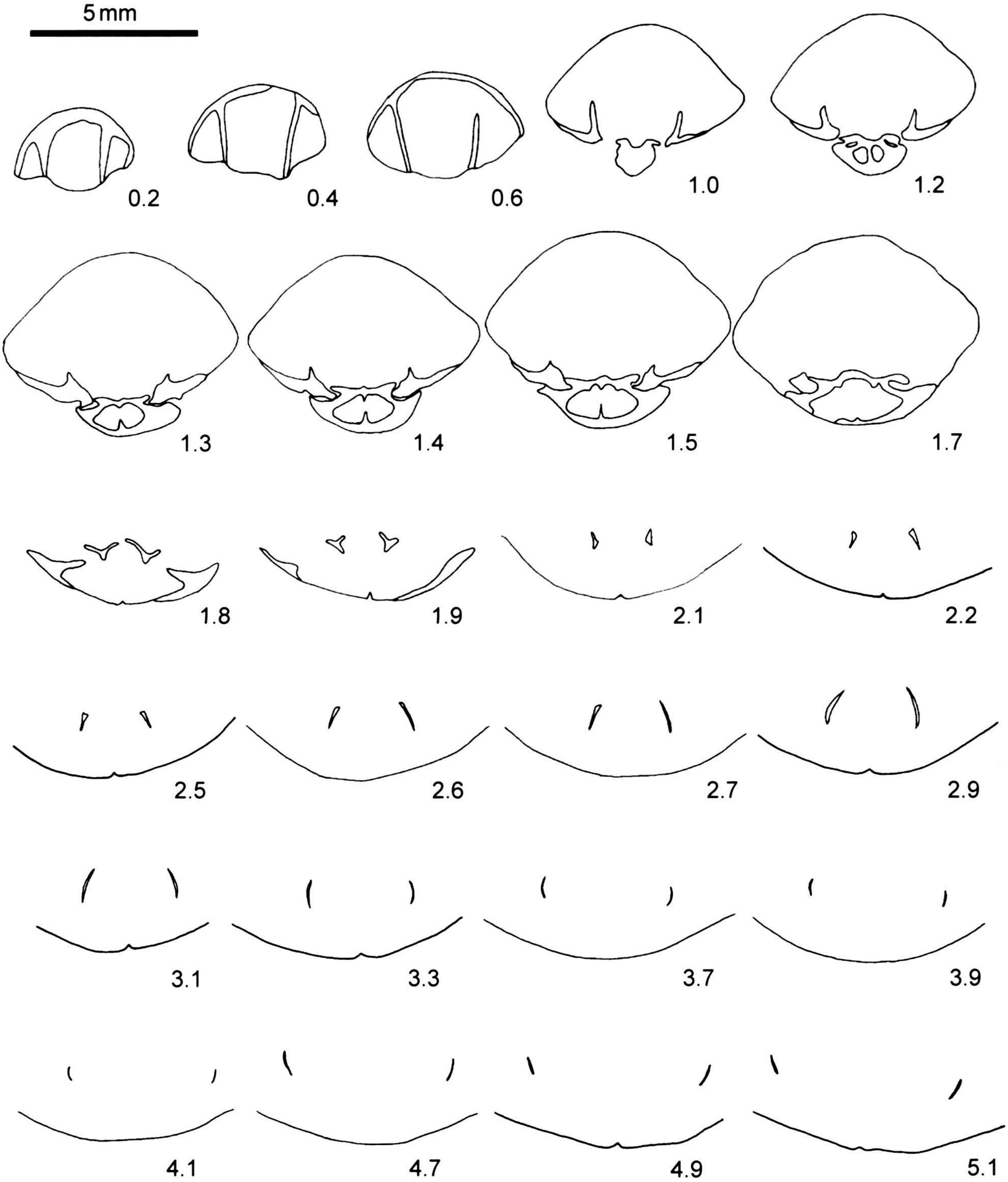

Fig. 2. *Psilothyris tamarindus* (J. de C. Sowerby 1836). Transverse serial sections through specimen RGF VR 67/12 from the Lower Aptian, Faca Vajali, Eastern Serbia, Carpatho-Balkanides. Dimensions (in mm): L = 14.2, W = 14.3, T = 7.8. Numbers refer to distance in mm from ventral apex.

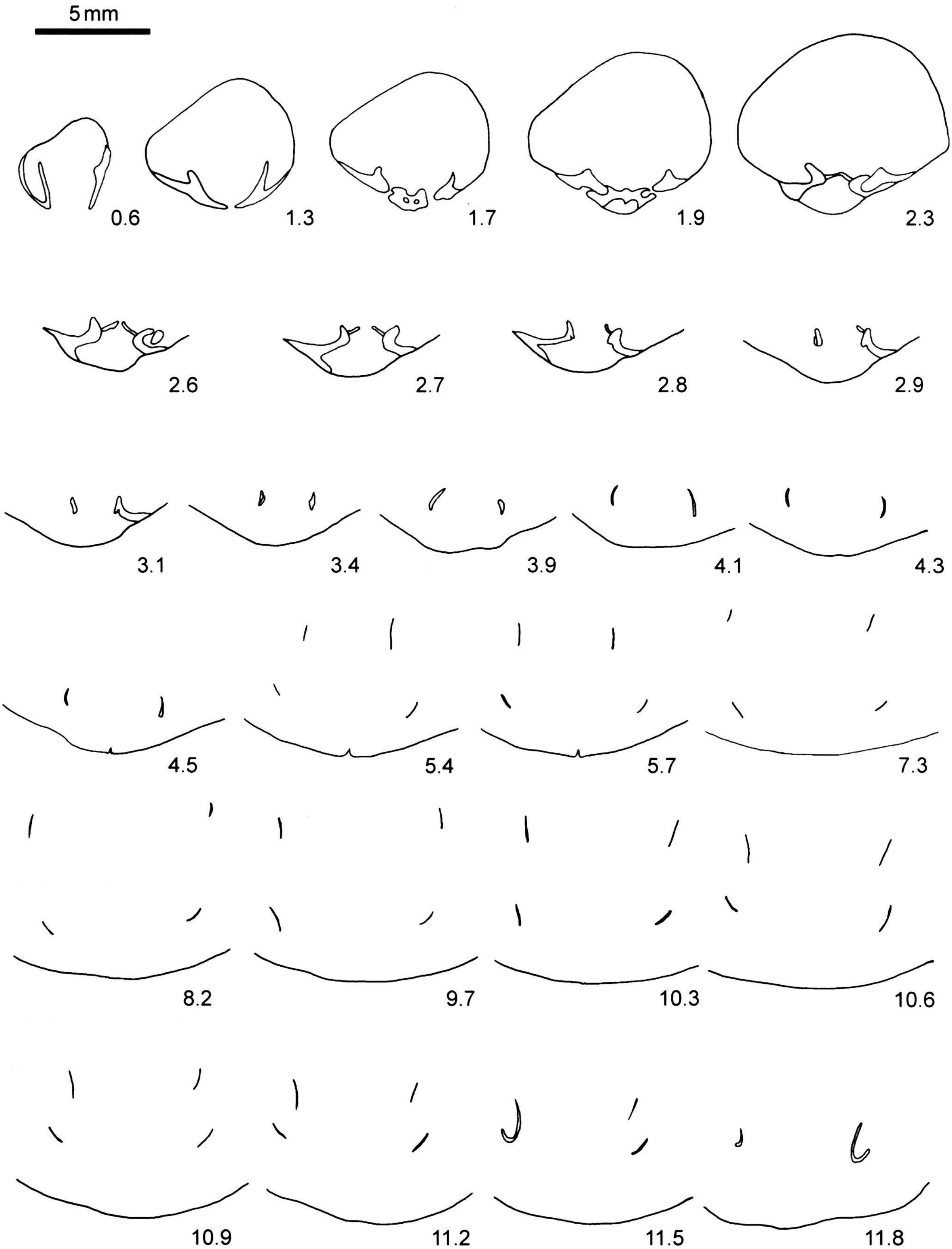

Fig. 3. *Psilothyris tamarindus* (J. de C. Sowerby 1836). Transverse serial sections through specimen RGF VR 67/11 from the Lower Aptian, Faca Vajali, Eastern Serbia, Carpatho-Balkanides. Dimensions (in mm): L = 14.9, W = 15.4, T = 9.6. Numbers refer to distance in mm from ventral apex.

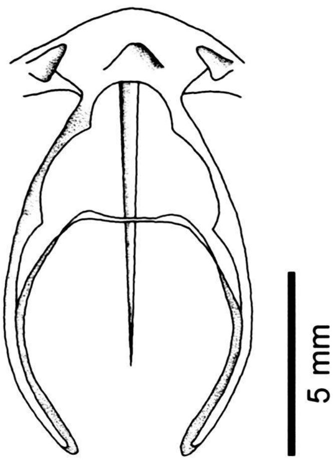

Fig. 4. Reconstruction of the dorsal internal features and the loop of *Psilothyris tamarindus* (J. de C. Sowerby 1836) from the serial sections of specimen RGF VR 67/11 shown in Fig. 3.

Dimensions of figured specimens (in mm). RGF VR 67/6, L = 17.6, W = 17.5, T = 10.8; RGF VR 67/8, L = 15.3, W = 14.5, T = 8.7; RGF VR 67/13, L = 13.5, W = 12.4, T = 6.3.

Distribution. Hauterivian of Switzerland, Caucasus and Crimea, Lower Barremian of Kopetdag (Trans-Caspian Region), Lower Aptian of Romania (southern Dobrogea), and eastern Serbia, Upper Aptian of Sardinia and southern France (Corbières), Aptian (Lower Greensand) of England.

Genus *Timacella* n. gen.

Type species. Waldheimia (Zeilleria) timacensis Antula 1903, Middle Neocomian, eastern Serbia.

Derivation of name. From the Timok river, eastern Serbia.

Diagnosis. Semi-ribbed biconvex shell of medium size with elongate oval to rarely subcircular outline. Beak small, erect with mesothyrid circular foramen. Fold and sulcus not developed. Anterior commissure rectimarginate, crenulate. Internal characteristics as in *Psilothyris.*

Distribution. Upper Barremian of the Carpatho-Balkanides, eastern Serbia.

Remarks. The new genus is similar to *Luppovithyris* Lobacheva known from the Hauterivian of the Kopetdag, Trans-Caspian Region (Lobacheva 1990a, 1990b), but *Timacella* n. gen. is distinguished by having coarse and less numerous subangular ribs. Internally, it differs by shorter dental lamellae, less developed hinge teeth, longer and lower median septum, which supports septalium only in its posterior part and by arched and fused inner hinge plates.

The main external character that distinguishes *Timacella* n. gen. from smooth-shelled *Psilothyris* is its ribbing only in the anterior half of the shell.

Timacella timacensis (Antula 1903)
Pl. 1, Fig. 4–8; Pl. 3, Fig. 1–5; Fig. 5–8

1903 *Waldheimia (Eudesia) timacensis* n. sp.; Antula: 50, Pl. 1, fig. 8–14
1930 *Waldheimia (Eudesia) timacensis* Antula; Petković: 106, pl. 3, fig. 5
1953 *Waldheimia (Eudesia) timacensis* Antula; Sučić: 110, pl. 3, fig. 8–10
1978 *Waldheimia timacensis* Antula; Jankičević: 129, 155

Neotype (designated herewith). Specimen RGF 25/15, Pl. 1, Fig. 4, (the original collection of Antula is lost) from the Upper Barremian of Crnoljevica, eastern Serbia, Carpatho-Balkanides.

Material. 33 complete specimens.

Description. External morphology. Medium sized shell, up to 18.6 mm in length, elongate oval to circular outline. In immature specimens, both valves are moderately and regularly convex. With the growth, valves increase in thickness so that old or gerontic specimens become almost globose in shape. Dorsal valve more convex. Maximum width at midlength. Maximum thickness in the middle or in the posterior third of valves. Beak small and low, in close contact with dorsal umbo, erect with a small circular foramen of mesothyrid type. Beak ridges sharp and short. Small deltidial plates disjunct. Interarea moderately developed. Anterior and lateral commissures straight. 10–18 subangular ribs ornament anterior half of the shell surface, while the posterior half is smooth. Median septum occupying about 0.55 of valve length. Concentric growth lines are occasionally present in the anterior half of valves.

Internal morphology. Four specimens have been sectioned, two of them are figured (Fig. 5, 6). Dental lamellae slightly divergent, very short, and disappear before the dorsal valve arises. Deltidial plates disjunct. Hinge teeth elongated and inserted at an angle of 40 degrees into narrow sockets. Concave septalium resting on the median septum developed posteriorly. Outer hinge plates broad and thin, subhorizontal to slightly inclined toward dorsal valve, gradually widening toward crural bases, leaning on inner socket ridges. Crural bases massive, triangular in shape, directed dorsally. Inner hinge plates anteriorly arched and fused forming a ridge in suspended septalium. Crural processes moderately high, ventrally oriented. Descending branches with a thickened portion. Transverse band high and fairly broad, thin, flat and centrally inflected in cross-section. Median septum low. Loop dalliniform, thin, with thickened descending branches, widest medially, extending about 0.80 of dorsal valve length. No spines observed on the loop.

Dimensions of figured specimens (in mm). Neotype RGF VR 25/15, L = 15.4, W = 11.2, T = 12.4; RGF VR 25/16, L = 16.1, W = 13.4, T = 12.8; RGF VR 25/2, L = 15.0, W = 13.6, T = 9.5; RGF VR 25/19, L = 15.0, W = 13.3, T = 8.8; RGF VR 25/10, L = 15.0, W = 13.8, T = 9.0. Thirty-three specimens were measured (Fig. 8).

Remarks. The species can be compared with semi-ribbed *Luppovithyris ovalis* Lobacheva from the Upper Hauterivian of Kopetdag. The latter species is distinguished from *T. timacensis* by its generally larger size, finer and numerous ribs (18–30), fold at anterior end, and much higher median septum.

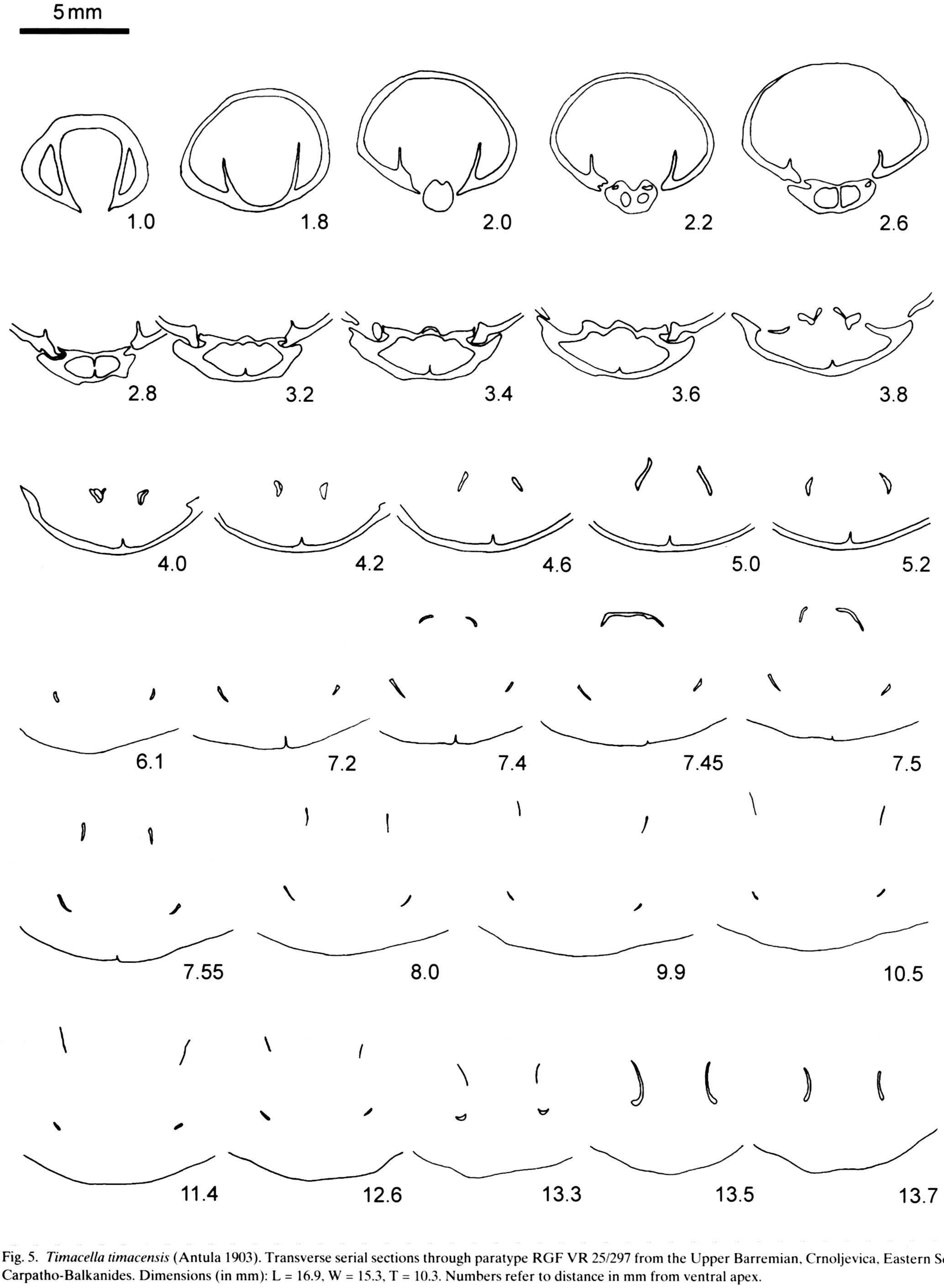

Fig. 5. *Timacella timacensis* (Antula 1903). Transverse serial sections through paratype RGF VR 25/297 from the Upper Barremian, Crnoljevica, Eastern Serbia, Carpatho-Balkanides. Dimensions (in mm): L = 16.9, W = 15.3, T = 10.3. Numbers refer to distance in mm from ventral apex.

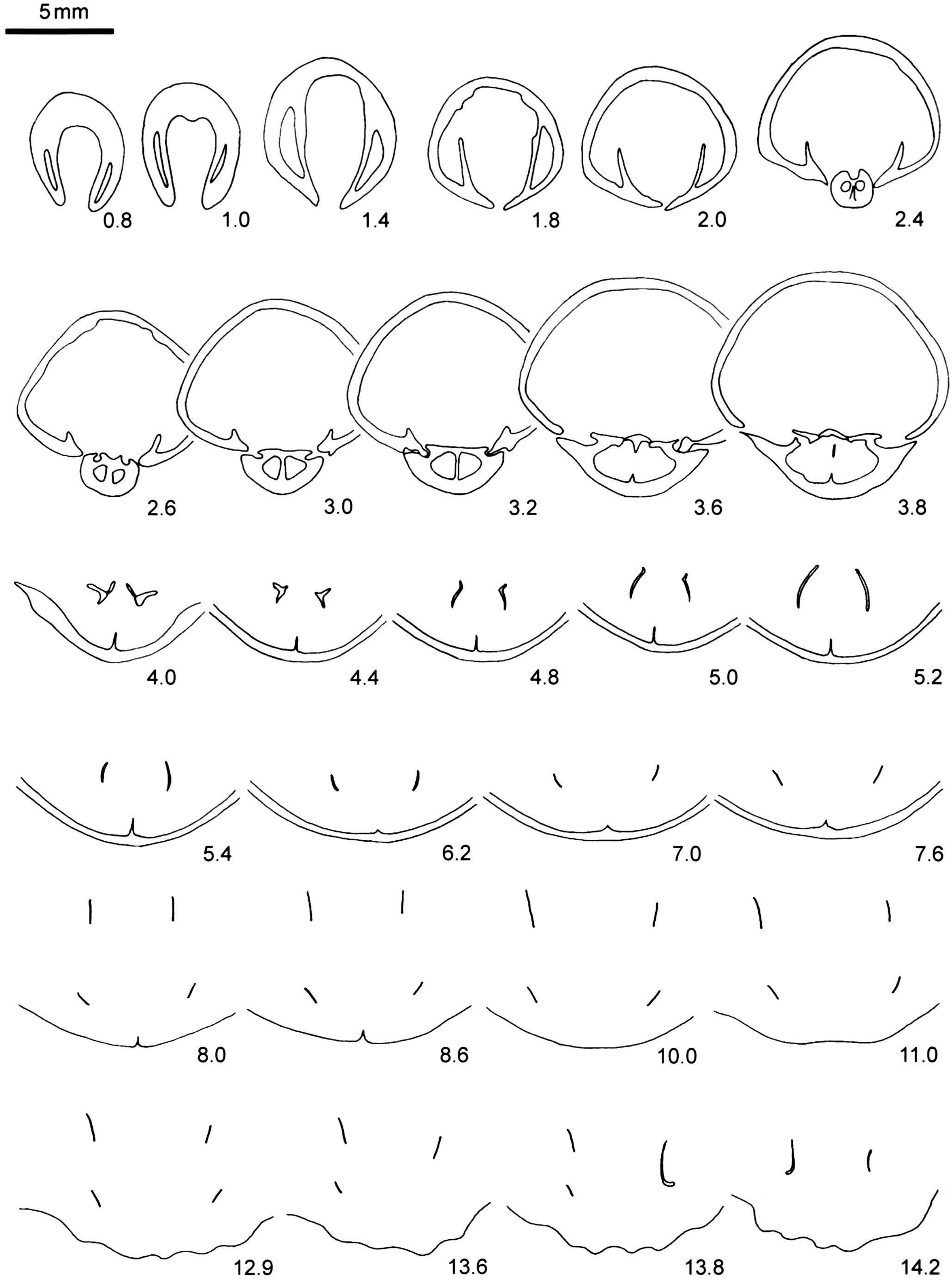

Fig. 6. *Timacella timacensis* (Antula 1903). Transverse serial sections through paratype RGF VR 25/6 from the Upper Barremin, Crnoljevica, Eastern Serbia, Carpatho-Balkanides. Dimensions (in mm): L = 17.2, W = 15.0, T = 11.6. Numbers refer to distance in mm from ventral apex.

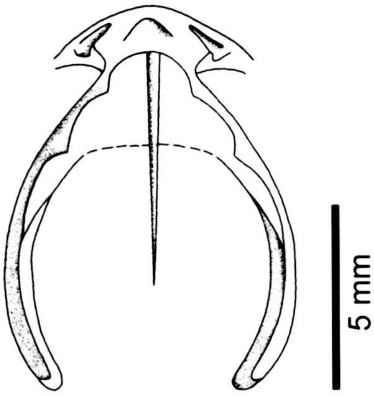

Fig. 7. Reconstruction of the dorsal internal features and the loop of *Timacella timacensis* (Antula 1903) from the serial sections of specimen RGF VR 25/297 shown in Fig. 5.

3. Comparison of *Psilothyris* and *Timacella*

Sandy (1986a, 1986b), Manceñido (1989), Lobacheva (1990b) and Calzada & Urquiola (1998) believed that *Tamarella* Owen 1965 is a junior subjective synonym of *Psilothyris*. We support the same opinion.

Psilothyris and *Timacella* n. gen. have identical internal features. The reconstructions of the loop of both genera show the thickening of the descending branches, which is extremely rare among long-loop brachiopods, and according to our knowledge this is the only known example. Owen (1965) stated "that this thickening may be the remains of an early connecting band or attachment". The loop of *Psilothyris* is wider than the one in *Timacella*. Based on 18 reconstructions of the loop of one of the Middle Jurassic terebratulid species, Radulović (1991) shows that the width and shape of the loop may considerably vary. The main external character that distinguishes the two genera is the smooth shell of *Psilothyris*.

The other Lower Cretaceous genus, which much resembles *Psilothyris*, is *Advenina* Sandy. The development of a median ridge anteriorly in the septalium of *Psilothyris* can be distinguished from the broad concave septalium of *Advenina* (Sandy, 1986b).

In its external and internal features *Psilothyris* is very close to the Bathonian-Hauterivian genus *Rugitela* Muir-Wood, but differs from it in a much shorter and lower median septum.

The series of transverse sections of our two specimens of *Psilothyris tamarindus* from the Carpatho-Balkanides of eastern Serbia does not show the overlapping hinge plates. This feature, very frequent in American and British representatives of the genus *Psilothyris*, seems to be of minor taxonomic significance and may be specifically variable in *Psilothyris*.

According to the present knowledge ten species known from Berriasian to Albian are assigned to the genus *Psilothyris*. This genus has a world-wide distribution in shallow shelf environments. All of the species are with smooth shell, more or less developed fold, and in all with known interior structure the hinge plates are fused and arched anteriorly. Neither of the species shows traces of incipient ribbing.

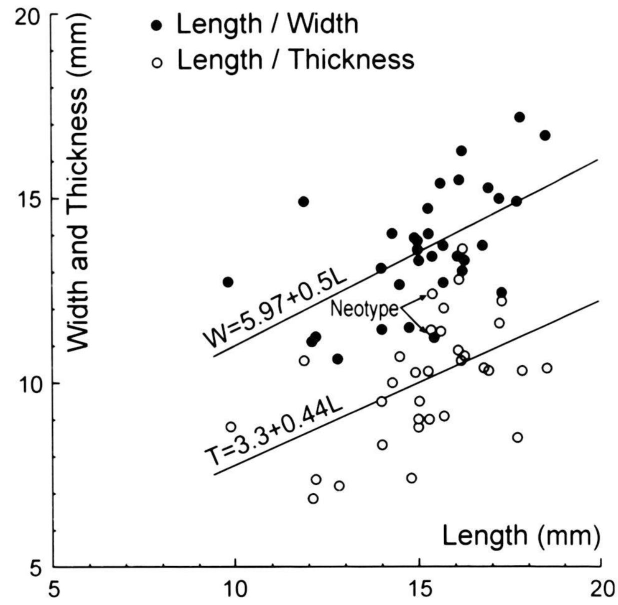

Fig. 8. *Timacella timacensis* (Antula 1903). Scatter plots for shell measurements of 33 specimens from the Upper Barremian, Crnoljevica, eastern Serbia, Carpatho-Balkanides.

Until now, the new genus *Timacella* is monospecific, reported only from a few localities of Upper Barremian in eastern Serbia. Further studies of the Urgonian fauna of the Carpatho-Balkanides will prove whether it is an exclusively endemic species or whether other possible representatives have a larger geographic distribution. The shell of *T. timacensis* is always semi-ribbed. Although a relatively large number of specimens from different localities have been found, no one had a smooth shell.

We think that all the species belonging to either *Psilothyris* or *Timacella* have smooth, or semi-ribbed shells, respectively. Therefore, there is scarcely any doubt that both „species" considered here are different morphotypes of the same species.

4. Shell Microstructure

The first data on the microstructure of the genus *Psilothyris* were published by Smirnova (1984), most probably based on her study of *Psilothyris cegemensis* (Moisseev in Smirnova 1960) with 20–25 µm fibre dimensions. Later (1990), she assigned this species to the genus *Advenina*.

Psilothyris tamarindus examined by us has shown that the shape of fibres is rounded rhomboidal, 10–12.5 µm wide (dimension of a fibre means its width along the longer diagonal in the cross-section of the fibres; to avoid inaccurate data, measurements, if it is possible, are always taken in the plane of symmetry).

Table 1. Measurements of the elements in the shell microstructure in μm

Species	*Psilothyris tamarindus*	*Timacella timacensis*
Thickness of the primary layer	20–25	45–60
Thickness of the secondary layer	175–200	170–215
Thickness of the tertiary layer	62.5–75	39–50
Width of the secondary fibres	10–12.5	10–12.5
Width of the fibres in the inner hinge plate	10–12.5	10–12.5
Width of the fibres in the hinge tooth	5–7.5	5–7.5
Width of the fibres in the outer hinge plate	5–6.25	5–6.25
Width of the fibres in the crural base	3.75–5	3.75–5

The shell wall in both species, *Psilothyris tamarindus* and *Timacella timacensis,* consists of three layers: primary, secondary, and tertiary layer.

The primary layer is preserved only where the shell is covered with sediment. This layer of granular structure consists of fine-grained calcite, sharply divided from the secondary layer. The thickness of the primary layer in *Psilothyris tamarindus* is smaller (20–25 μm) than that in *Timacella timacensis* (45–60 μm).

The secondary (fibrous) layer is 175–200 μm thick in *Psilothyris tamarindus* and somewhat thicker, 170–215 μm, in *Timacella timacensis*. Fibres of the secondary layer in both species are built up of a rounded rhomboidal outline in cross-section with a width of 10–12.5 μm.

The tertiary (prismatic) layer is partially developed on the inner surface of the secondary layer and consists of one row of calcite crystals. *Psilothyris tamarindus* has somewhat greater thickness of 62.5–75 μm instead of 39–50 μm in *Timacella timacensis*.

The internal skeletal structures, except in the inner hinge plates, consist of fibres smaller than those composing the secondary layer and have the same outline. Their dimensions are identical in both species. The inner hinge plates are built of fibres that are equal in size and form to those in the secondary layer. Fibres forming the hinge teeth are the biggest and are 5–7.25 μm wide. Fibres building outer hinge plates are 5–6.25 μm wide, while fibres in crural bases are smaller, 3.75–5 μm wide.

In the two species studied, minor differences have been observed in thicknesses of the primary, secondary and tertiary layers (Table 1).

5. Conclusions

Upper Barremian semi-ribbed *Timacella timacensis* and Lower Aptian smooth-shelled *Psilothyris tamarindus* are found in the shallow-water limestones of the eastern Serbian Carpatho-Balkanides and are described in this work.

The series of transverse sections and ultrastructural examinations show these two species having different external morphology but very similar internal structure. The fibres building up the secondary shell layer and the internal skeletal elements (outer hinge plates, crural bases, inner hinge plates, hinge teeth) are identical in the two species.

The only minor dissimilarity is observed in the thicknesses of primary, secondary and tertiary shell layers of the two species.

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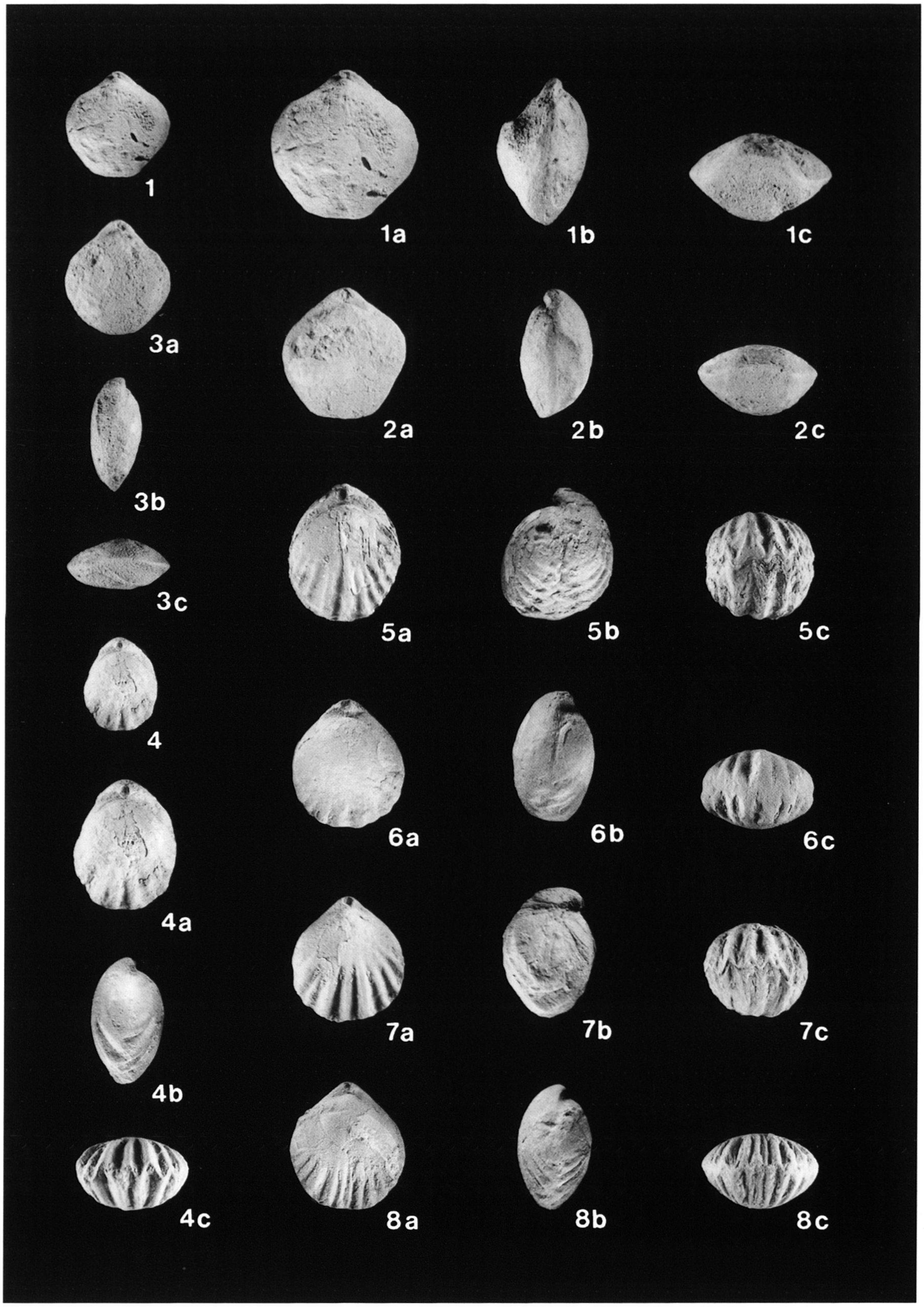
Plate 1

Fig. 1–3. *Psilothyris tamarindus* (J. de C. Sowerby 1836), Lower Aptian, Faca Vajali, eastern Serbia, Carpatho-Balkanides. 1, RGF VR 67/6. 2, RGF VR 67/8. 3, RGF VR 67/13.
Fig. 4–8. *Timacella timacensis* (Antula, 1903), Upper Barremian, Crnoljevica, eastern Serbia, Carpatho-Balkanides. 4, neotype, RGF VR 25/15. 5, paratype, geronticspecimen, RGF VR 25/16. 6, paratype, RGF VR 25/2. 7, paratype, RGF VR 25/19. 8, paratype, RGF VR 25/10.

All × 1.5, except Fig. 1 and 4, × 1; a = dorsal view, b = lateral view, c = anterior view.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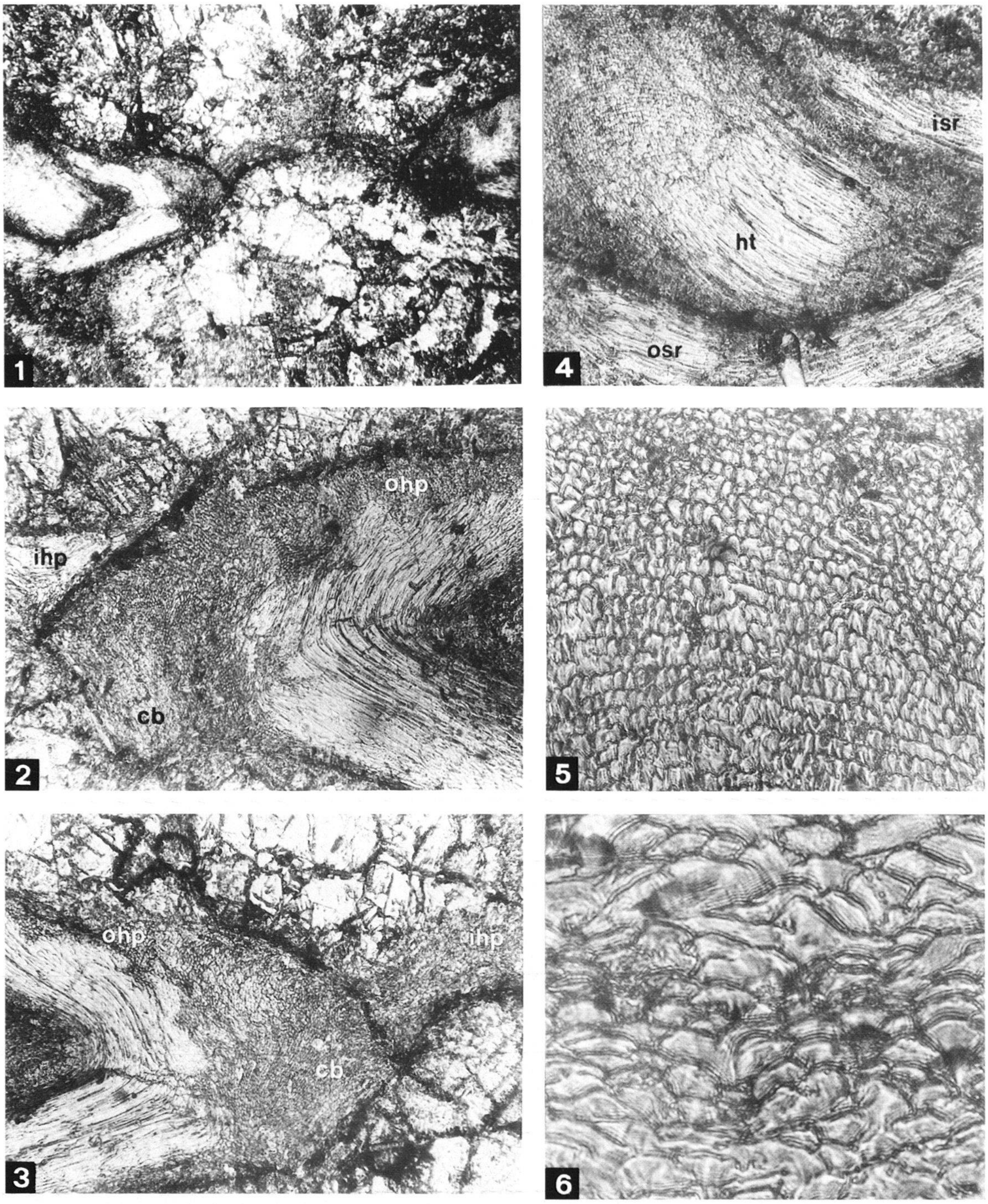

Plate 2

Fig. 1–6. *Psilothyris tamarindus* (J. de C. Sowerby 1836), Lower Aptian, Faca Vajali, eastern Serbia, Carpatho-Balkanides. Micrographs of transverse sections of the shell. Specimen RGF VR 67/7. 1: arched septalium in the anterior part of the shell is shown; × 25. 2, 3: ohp = outer hinge plate, cb = crural base, ihp = arched inner hinge plate; × 80. 4: ht = hinge tooth, isr = inner socket ridge, osr = outer socket ridge; × 80. 5: fibres of hinge tooth; × 260. 6: section shows the shape of fibres in the secondary (fibrous) layer; × 650.

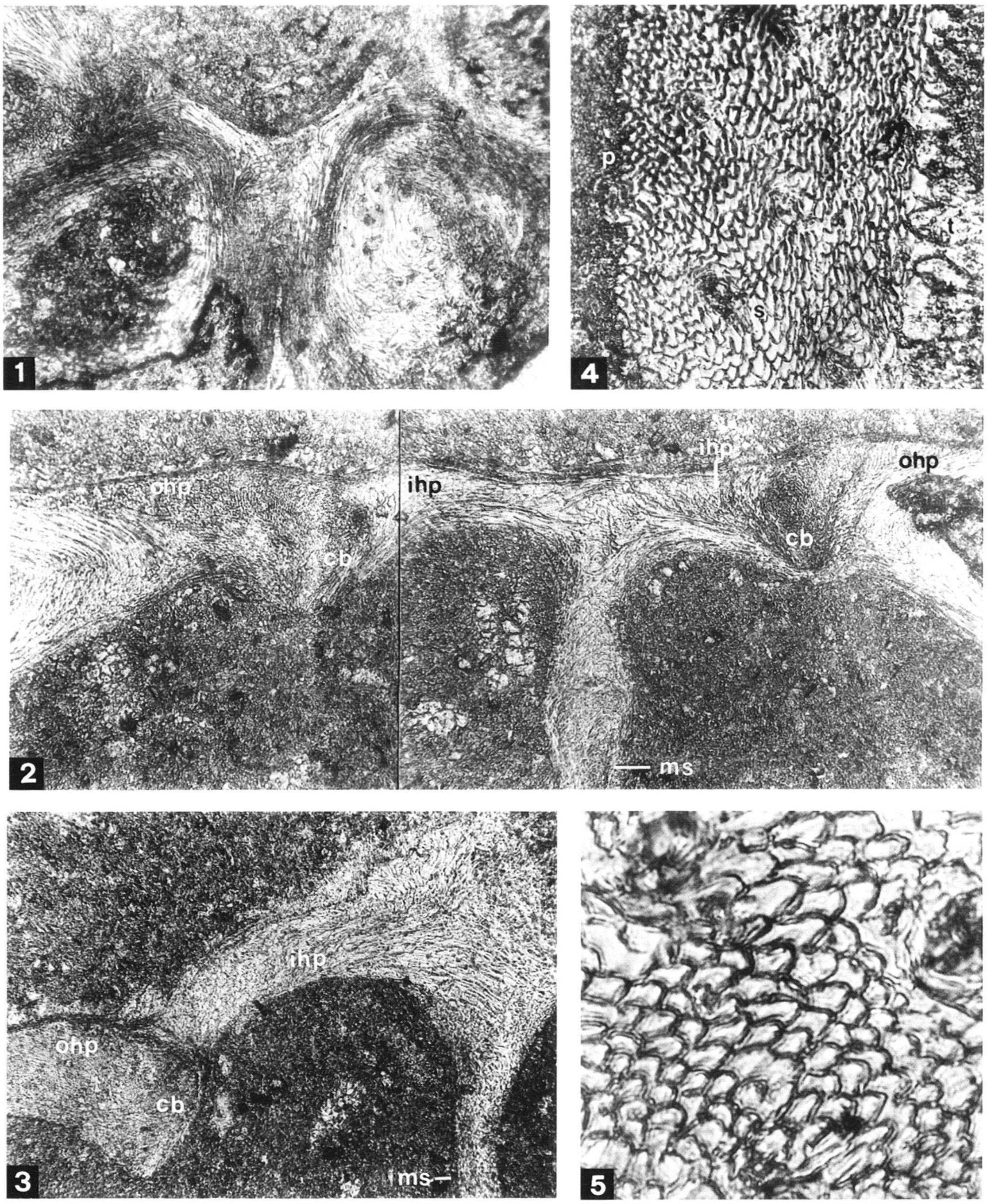

Plate 3

Fig. 1–5. *Timacella timacensis* (Antula 1903), Upper Barremian, Crnoljevica, eastern Serbia, Carpatho-Balkanides. Micrographs of transverse sections of the shell. Paratype RGF VR 25/18. 1: concave septalium in the posterior part of shell is shown; × 80. 2: ohp = outer hinge plate, cb = crural base, ihp = inner hinge plate, ms = median septum; × 80. 3: ohp = outer hinge plate, cb = crural base, ihp = arched inner hinge plate, ms = median septum; × 80. 4: p = primary layer, s = secondary (fibrous) layer, t = tertiary (prismatic) layer; × 260. 5: section showing the shape of fibres and punctae in the secondary (fibrous) layer; × 650.