

# The origin of the Pycnodontinae and relationship between gryphaeas and true pycnodontes

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Berriasian (Early Cretaceous) oyster *Pycnogryphaea weberae* from Crimea is one of the earliest known pycnodontine oysters. Examination of shell morphology and microstructure of this species shows that it shares characters of the subfamilies Gryphaeinae and Pycnodontinae. Shell microstructure of *Pycnogryphaea weberae* lacks vesicular structure and is similar to microstructure of the genus *Gryphaea*. At the same time the shell of this species possesses morphological characters typical of pycnodontines: development of chomata and well-defined circumferential curb. *Pycnogryphaea weberae* is regarded as a transitional taxon between the subfamilies Gryphaeinae and Pycnodontinae and referred herein to a new genus *Pycnogryphaea* within the Pycnodontinae. This suggests that the subfamily Pycnodontinae likely originated from the Late Jurassic representatives of the genus *Gryphaea* (Gryphaeinae) in Berriasian. First pycnodontines preserved shell microstructure of the genus *Gryphaea* but developed chomata along all the perimeter of both valves.

Key words: Bivalvia, Gryphaeinae, Pycnodontinae, Cretaceous, Berriasian, Crimea.

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## Introduction

The subfamily Pycnodontinae was first proposed by Stenzel in 1959. Its original diagnosis includes: well-defined commissural shelf, proximally delimited by a circumferential curb; chomata short to long, branching and vermiculate; occurrence of vesicular structure; and absence of prismatic shell layer, except for the genus *Neopycnodonte* Stenzel, 1971 (Fig. 1). The subfamily Pycnodontinae ranges from the Early Cretaceous to Recent (Stenzel 1971). Stenzel (1971: N1096) emphasized that the main morphological characteristic of the subfamily Pycnodontinae is the occurrence of vesicular shell layer.

Harry (1985), Malchus (1990), Cooper (1992), and Ivanov (1995) later clarified the diagnoses of supraspecific taxa within the subfamily Pycnodontinae. Cooper (1992) was the first to propose a hypothesized relationships within the subfamily Pycnodontinae on the basis of the shell morphology. In this model, genus *Bilobissa* Stenzel, 1971 (Cooper considered *Bilobissa* as a genus within the Pycnodontinae; herein *Bilobissa* is considered as a subgenus of *Gryphaea* [Gryphaeinae] as in original description of Stenzel [1971]) and genus *Texigryphaea* Stenzel, 1959 are closely related (Cooper

1992: fig. 1). Furthermore, the phylogenetic affinities of the subgenus *Bilobissa* as closely related to the Pycnodontinae were already proposed by Stenzel (1971: N1099) in its subgeneric description. However, the stratigraphic distribution of subgenus *Bilobissa* and genus *Texigryphaea* ranges from Middle to Late Jurassic, and Albian to Cenomanian, respectively, whereas other oysters from the subfamily Pycnodontinae were absent through Berriasian and Albian successions. This problem of a large temporal gap in the occurrence of Pycnodontine oysters was later resolved with the discovery of the species *Pycnodonte miranda* Bogdanova, 1980, in the Berriasian–Valanginian successions of the Mangyshlak Region (north-western Kazakhstan), as well as *Gryphaea weberae* Yanin in Tschelzova, 1969 in the Berriasian of Crimea. Later, Bogdanova (in Arkadiev et al. 1997) and Yanin (in Arkadiev et al. 2012) transferred *G. weberae* to the genus *Pycnodonte* Fisher de Waldheim, 1835. Thus, *Pycnodonte weberae* is one of the earliest pycnodontine oysters.

The aim of this study is to re-examine the morphology and microstructure of the species *Pycnodonte weberae* in order to understand its taxonomic affinities, and more generally the early evolution of the Pycnodontinae. In this work, previously published data (Tschelzova 1969; Arkadiev et al.

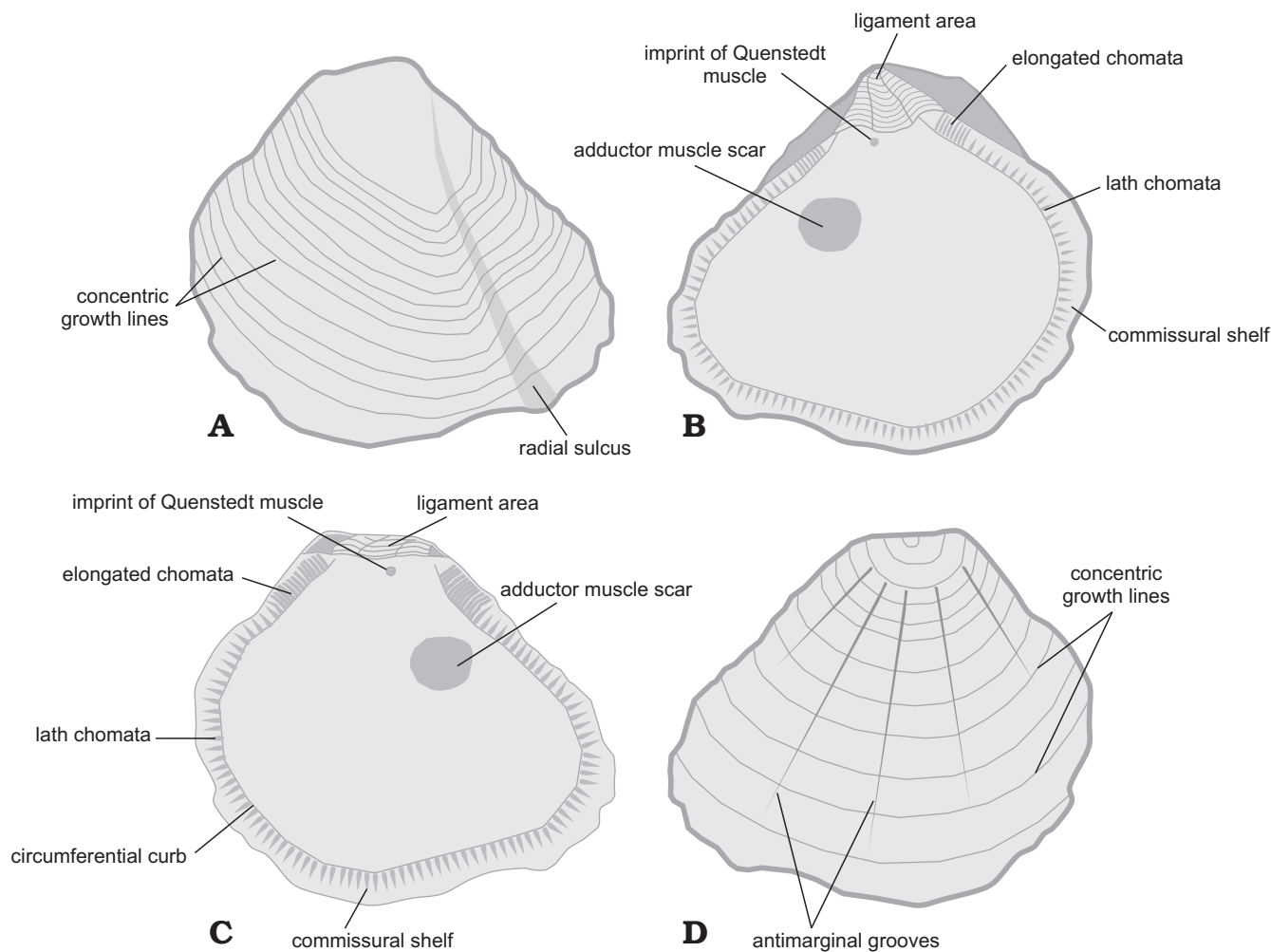


Fig. 1. Schematic drawing illustrating shell morphology of *Pycnogryphaea weberae* Yanin in Tschelzova, 1969. Left valve in inner (A) and outer (B) views; right valve in inner (C) and outer (D) views. The image is given approximately in natural size.

1997, 2012) are re-examined and backed by new data on the microstructure of the species *Pycnodonte weberae* from the Berriasian successions of Crimea.

**Institutional abbreviations.**—CP MSU, Chair of Palaeontology, Moscow State University, Moscow, Russia; IPGG SB RAS, Trofimuk Institute of Petroleum Geology and Geophysics Siberian Branch of Russian Academy of Sciences, Novosibirsk, Russia; TsSGM, Central Siberian Geological Museum, Novosibirsk, Russia; VSEGEI, All Russian Research Geological Institute, St. Petersburg, Russia.

**Other abbreviations.**—Conv, convexity of the shell; Conv/L, convexity coefficient; H, shell height; L, shell length; L/H, elongation coefficient.

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## Material and methods

The studied material was collected by Tamara N. Bogdanova (VSEGEI) in the Berriasian sections of Crimean Mountains (*Pseudosubplanites grandis* Subzone in the section Sarysu river; *Dalmasiceras tauricum* Subzone in the section Balki village; lower part of *Riasanites crassicostatum* Subzone in the section Chernokamenka village; beds with *Symphythyris arguinensis* in sections Balki village and Kuchki village; beds with *Zeillerina baksanensis* corresponding the uppermost Berriasian in the section Mezhgorye village) (Figs. 2, 3). The material consists of 83 left and 39 right valves of the species *Pycnogryphaea weberae*.

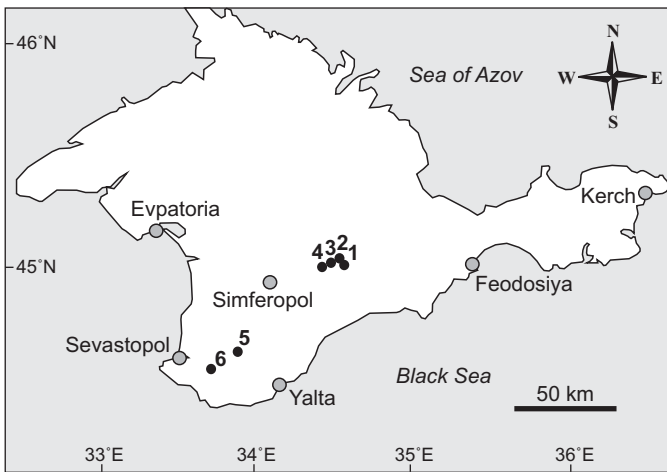


Fig. 2. Geographical position of the studied oysters locations. 1, Chernokamenka village; 2, Sarysu river; 3, Balki village; 4, Mezhgorye village; 5, Solnechnoselye village; 6, Kuchki village.

Crimean upper Maastrichtian species *Phygraea vesicularis* (Lamarck, 1806) and *Pycnodonte mirabilis* (Rousseau, 1842) and Paleogene species *Phygraea pseudovesicularis* (Gümbel, 1861), pycnodonteine oysters were collected by INK together with Vladimir V. Arkadiev (St. Petersburg State University, Russia) and used as comparative material in the microstructural studies.

In order to understand the intraspecific variability of the species *Pycnogryphaea weberae*, the following morphometric parameters were measured on specimens from the *Dalmasiceras tauricum* Subzone (the section Balki village): shell height, shell length and convexity of the shell; calculated parameters include: elongation coefficient and convexity coefficient. Distributions graphs were prepared on the basis of the previously mentioned parameters using the freely distributed software Past 3 (Hammer et al. 2001)

The microstructure of the shells was examined in thin sections under light microscope Olympus BX60. Shell photographs were made after whitening with ammonium chloride (NH<sub>4</sub>Cl) using a camera Canon EOS 60D.

The morphological and microstructure terminology is taken from Stenzel (1971), Carter (1990), Carter et al. (2012) and Koppka (2015). The term “furcate” microstructure comes from the work of Tschelzova (1969). In longitudinal section, furcate microstructure consists on a system of tree-like branching of vertical, large, irregular calcite crystals producing irregular embranchment in the upper part of the layer (Tschelzova 1969: 25, fig. 13). Interspaces between vertical and inclined crystals are filled by thin parallel calcite lamellas (0.01–0.02 mm), which in turn are more or less parallel to the shell surface. Extinction is heterogeneous.

## Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Subclass Autobranchia Grobben, 1894

Stage	Mediterranean region (Reboulet et al. 2014; Frau et al. 2015)	Crimean Mountains (Arkadiev et al. 2017a, b)	Distribution of <i>P. weberae</i>	
Vln	<i>Thurmanniceras petransiens</i>			
Berriasian	Subthurmannia boissieri	<i>Thurmanniceras otopeta</i>	?	
		<i>Thurmanniceras alpillensis</i>		
		<i>Berriasella picteti</i>	Subzone <i>Berriasella callisto</i>	4
			?	
			beds with <i>Symphythyris arguinensis</i>	6
	Subzone <i>Riasanites crassicostatum</i>	1		
	<i>Malbosciceras paramimounum</i>	Subzone <i>Neocosmoceras eythymi</i>		
		?		
	Subthurmannia occitanica	<i>Dalmasiceras dalmasi</i>	Subzone <i>Dalmasiceras tauricum</i>	3
			beds with <i>Tirnovella occitanica</i> and <i>Retowskiceras retowskyi</i>	
<i>Berriasella privasensis</i>		?		
	<i>Subthurmannia subalpina</i>	beds with <i>Malbosciceras chaperi</i>	5	
<i>Berriasella jacobi</i>		<i>Berriasella jacobi</i>	Subzone <i>Pseudosubplanites grandis</i>	2
	<i>Berriasella jacobi</i>			

Fig. 3. Subdivision of the Berriasian stage from Crimean Mountains correlated along with Mediterranean basin, and associated distribution of the species *Pycnogryphaea weberae* from the different localities. 1, Chernokamenka village; 2, Sarysu river; 3, Balki village; 4, Mezhgorye village; 5, Solnechnoselye village; 6, Kuchki village; Vln, Valanginian. Stratigraphy after Arkadiev et al. 2017a, b.

Cohort Ostreomorphi Férussac, 1822

Subcohort Ostreoini Férussac, 1822

Megaorder Ostreata Férussac, 1822

Superorder Ostreiformii Férussac, 1822  
(= Eupteriomorphia Boss, 1982)

Order Ostreida Férussac, 1822

Suborder Ostreidina Férussac, 1822

Superfamily Ostreoidea Rafinesque, 1815

## Family Gryphaeidae Vialov, 1936

## Subfamily Pycnodontinae Stenzel, 1959

Genus *Pycnogryphaea* nov.

*Etymology*: Combination of two gryphaeid generic names *Pycnodonte*, and *Gryphaea*, since the new genus shares characteristics of both.

*Type species*: *Gryphaea weberae* Yanin in Tschelzova, 1969, Berriasian of Crimea, section Sarysu river.

*Species included*: Type species only.

*Emended diagnosis*.—As for the type species (by monotypy).

*Description (microstructure)*.—Outer shell layer of left valve consists in furcate microstructure. Inner shell layer of left valve consists mainly in irregular complex crossed foliated microstructure with sublayers of simple regular foliated microstructure. Outer shell layer of right valve consists in prismatic microstructure. Inner shell layer of right valve consists in simple regular foliated and irregular complex crossed foliated microstructures with chomata influenced crossed foliated microstructure. Chambering absent. Vesicular microstructure absent.

*Remarks*.—Late Triassic to Late Jurassic (or even Early Cretaceous according to Zakharov 1966 and Kosenko 2017) *Gryphaea* Lamarck, 1801, (Gryphaeinae) characterized by a gryphaeid shell shape, orthogyrate beaked umbo, circular posterodorsally located posterior adductor muscle scar and radial grooves on the right valve, appears to be very similar to *Pycnogryphaea*. *Pycnogryphaea* differs from *Gryphaea* by chomata developed all along the circumferential curb. Due to the presence of chomata *Pycnogryphaea* is regarded here within the Pycnodontinae. However, it differs from other genera of the Pycnodontinae by the absence of vesicular structure in shell microstructure.

The Albian to Cenomanian *Texigryphaea* Stenzel, 1959, appears to be similar to *Pycnogryphaea* by the lath chomata developed along the entire circumferential curb. However, *Texigryphaea* differs by commonly anterodorsally compressed left valve with median radial keel. Several genera of the Pycnodontinae, such as *Crenostrea* Marwick, 1931 (Paleogene of New Zealand), "*Pycnodonte*" gr. *newberryi* (Stanton, 1893) (early Late Cretaceous of North America), *Labrostrea* Vialov, 1945 (Late Cretaceous–Paleogene, distributed worldwide), *Phygraea* Vialov, 1936 (Late Cretaceous–Paleogene, worldwide), and *Costeina* Vialov, 1936 (Late Cretaceous of North America and Europe) had developed a gryphaeid shell shape. However, all these taxa differ from *Pycnogryphaea* by the presence of a vesicular structure and chomata developed only near the ligament area. Another peculiar character of *Pycnogryphaea* is ab-

sence of simple herringbone regularly foliated structure typical for most Pycnodontinae (Aqrabawi 1993; Yakushin and Ivanov 2001).

The Late Jurassic *Circunula* Koppka, 2015, questionably referred by Koppka (2015) to the Pycnodontinae, recorded from the Oxfordian to Kimmeridgian of Switzerland and France, the Kimmeridgian of Germany and Crimea and the Tithonian of Czech Republic, differs from *Pycnogryphaea* by a large attachment area, the disappearance of chomata in adult growth stage and the non gryphaeid shell shape.

*Stratigraphic and geographic range*.—Berriasian of Crimea.

*Pycnogryphaea weberae* (Yanin in Tschelzova, 1969)

Fig. 4.

1969 *Gryphaea weberae* Yanin sp. nov.; Tschelzova 1969: 56, pl. 4: 6, 7–8 (microstructure).

1997 *Pycnodonte weberae* (Yanin in Tschelzova, 1969); Arkadiev et al. 1997: 78, pl. 18: 8.

2012 *Pycnodonte weberae* (Yanin in Tschelzova, 1969); Arkadiev et al. 2012: 251, pl. 43: 16.

*Type material*: Holotype CP MSU 331/16 (Tschelzova 1969: pl. 4: 6).

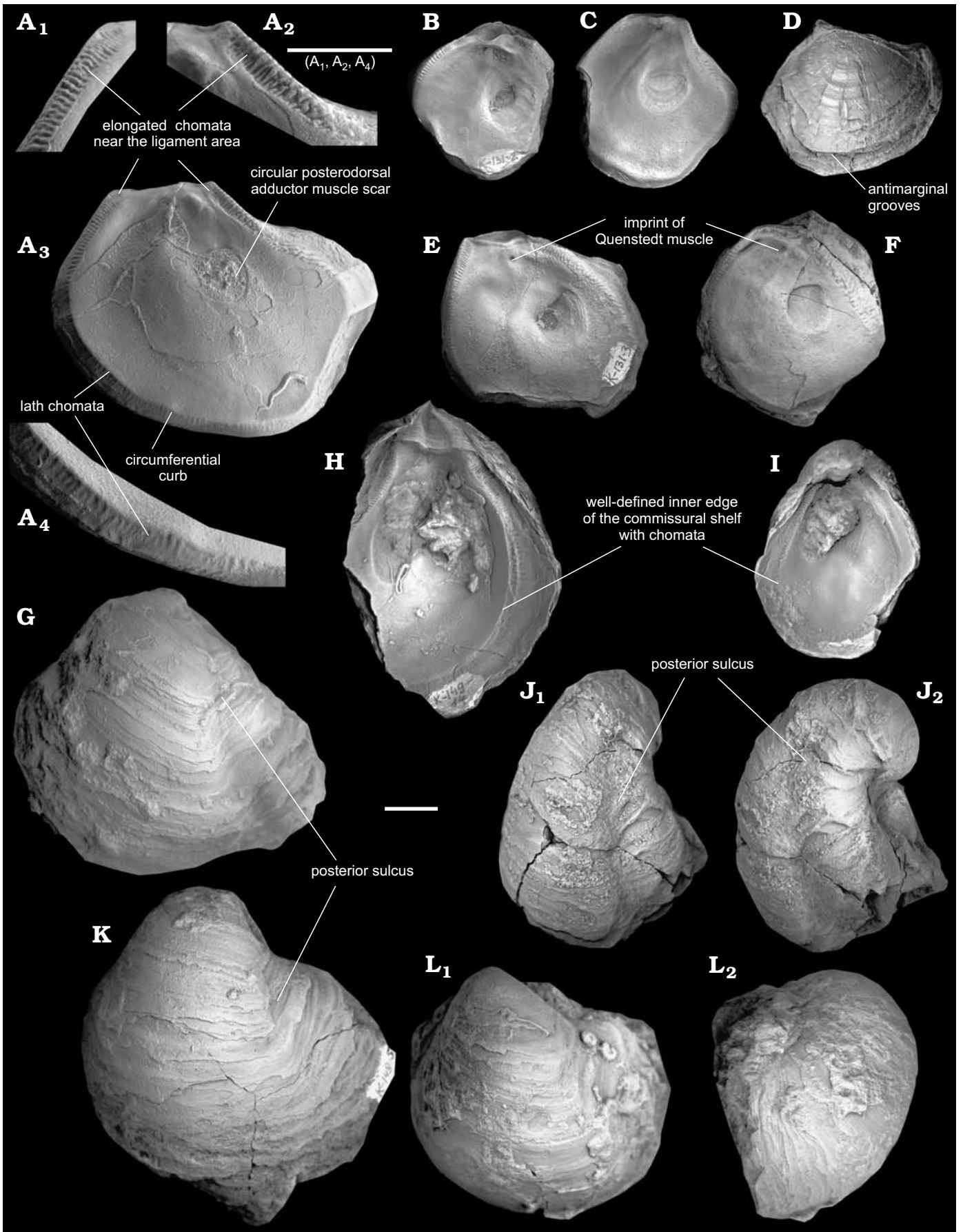
*Type locality*: Central Crimea, sections Sarysu river and Balki village.

*Type horizon*: Middle Berriasian.

*Material*.—11 left valves and 4 right valves, section Sarysu river, *Pseudosubplanites grandis* Zone; 15 left valves, section Solnechnoselye village, beds with *Malbosiceras chaperi*; 53 left valves and 22 right valves, section Balki village, *Dalmasiceras tauricum* Zone; 1 juvenile left valve and 2 right valves, section Chernokamenka village, lower part of the *Riasanites crassicostatum* Subzone; 1 left valve and 5 right valves, section Balki village, beds with *Symphythyris arguiniensis*; 1 left valve and 3 right valves, section Kuchki village, beds with *Symphythyris arguiniensis*; 1 left valve and 3 right valves, section Mezhgorye village, beds with *Zeillerina baksanensis* (base of the *Berriasella callipso* Subzone to the Berriasian–Valanginian boundary). All material is housed in the Central Siberian Geological Museum, and referenced as collection TsSGM 2088 (TsSGM 2088/1–110).

*Emended diagnosis*.—Shell medium-sized, strongly inequivalve and thick. Left valve gryphaeid, strongly convex with well-defined posterior sulcus and posterior flange, right valve flat or slightly concave. Outlines triangular or subtriangular. Attachment area very small. Left valve umbo prominent, rising well above hinge line. Both valves with concentric growth squamae, right valve with weak antimarginal grooves. Left valve lacks umbonal cavity. Ligament area triangular with triangular resilifer. Posterior adductor scar located posterodorsally, rounded (gryphaeid). Quenstedt muscle scar well distinguishable on right valve,

Fig. 4. Pycnodontin oyster *Pycnogryphaea weberae* (Yanin in Tschelzova, 1969) from Berriasian of Crimea, section Balki village, *Dalmasiceras tauricum* Subzone (A, C, D, F–L) and Mezhgorye village, beds with *Zeillerina baksanensis* (B, E). **A.** TsSGM 2088/28, interior of right valve (A<sub>3</sub>); elongated chomata near the hinge (A<sub>1</sub>, A<sub>2</sub>), simple lath chomata near the ventral margin of right valve (A<sub>4</sub>). **B.** TsSGM 2088/29, interior of right valve. **C.** TsSGM 2088/30, interior of right valve. **D.** TsSGM 2088/31, exterior of right valve. **E.** TsSGM 2088/34, interior of right valve. **F.** TsSGM 2088/32, interior of right valve. **G.** TsSGM 2088/3, exterior of left valve. **H.** TsSGM 2088/33, interior of left valve. **I.** TsSGM 2088/14, interior of left valve. **J.** TsSGM 2088/15, exterior of left valve (J<sub>1</sub>) and view from the posterior side (J<sub>2</sub>). **K.** TsSGM 2088/5, exterior of left valve. **L.** TsSGM 2088/2, exterior of left valve (L<sub>1</sub>) and view from the anterior side (L<sub>2</sub>). Scale bars 10 mm.



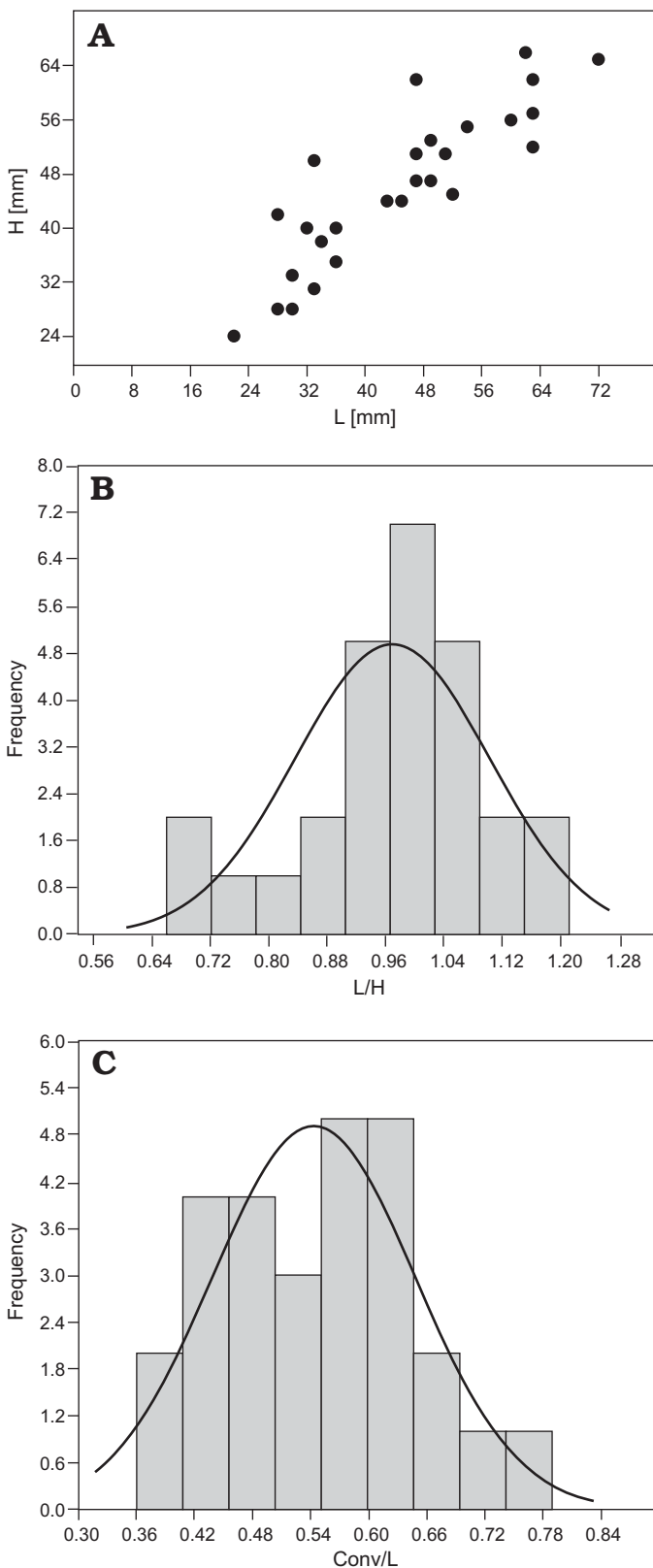


Fig. 5. Variability of pycnodontin oyster *Pycnogryphaea weberae* (Yanin in Tschelzova, 1969) from Berriasian of Crimea, section Balki village, *Dalmasiceras tauricum* Subzone. **A.** Length vs. height,  $N = 27$ . **B.** Length/height frequency,  $N = 27$ . **C.** Convexity/length frequency,  $N = 27$ . Conv, convexity of shell; Conv/L, convexity coefficient; H, shell height; L, shell length; L/H, elongation coefficient.

located ventrally from resilifer. Commissural shelf narrow, well-defined, delimited by circumferential curb. Chomata developed all along the circumferential curb. Elongated chomata located near ligament area, simple lath chomata developed below elongated chomata.

*Description.*—Left valve gryphaeoid, moderately to highly convex (convexity coefficient Conv/L in studied samples varies from 0.36 to 0.80; see Fig. 5C), triangular to oval in outline, sometimes with opisthogyrate beak, larger than the right valve; right valve flat or slightly concave. Examined specimens up to 66 mm high and up to 72 mm long (Fig. 5A); elongation coefficient (L/H) varies in studied sample from 0.66 to 1.22 (Fig. 5B). Left valve covered by commarginal growth lines; well-defined posterior sulcus. Attachment area very small (diameter up to 10 mm in shell with 42 mm high and 47 mm long; usually not distinguishable). Right valve with well-defined commarginal growth lines and antimarginal grooves.

*Ligament area:* small, triangular; initially prosogyrate in some specimens; resilifer triangular, weakly concave with slightly convex bourrelets on both valves, less elevated on the right valve. Plane of ligament area depends on the degree of beak development: from almost perpendicular to the commissure plane in shells with a well-developed beak, to subparallel to the commissure plane in shells having a non-developed beak.

*Internal shell characters:* Umbonal cavity absent. Posterior adductor muscle rounded, relatively small, postero-dorsal. Quenstedt muscle scar well distinguishable on the right valve, approximately located approximately under the resilifer (Fig. 4A–C, E, F). Commissural shelf narrow, well-defined, delimited by the circumferential curb. Chomata developed on commissural shelf all along the circumferential curb. Elongated chomata located near the ligament area, simple lath chomata developed below the elongated chomata.

*Microstructure:* Outer shell layer of left valve characterized by furcate microstructure (around 300  $\mu\text{m}$ ) (Fig. 6D). Inner shell layer of left valve characterized by different types of irregular complex crossed foliated microstructure: homogeneous to “mosaic” irregular complex crossed foliated (Fig. 6D), low angle irregular complex crossed foliated (Fig. 6B, E, F) and dominated by high angle irregular complex crossed foliated (Figs. 6C, C, E, 7A<sub>2</sub>). Myostracum of left valve with irregular simple prismatic structure (Fig. 7A<sub>2</sub>). Outer layer of right valve consists of coarse simple prismatic microstructure (around 100  $\mu\text{m}$ ) (Fig. 7B<sub>3</sub>). Inner layer consists of simple regular foliated microstructure (Fig. 7A<sub>3</sub>, A<sub>4</sub>, B<sub>2</sub>, B<sub>3</sub>) with areas of chomata-influenced crossed foliated microstructure (Fig. 7B<sub>2</sub>) lapsing to low angle irregular complex crossed foliated (Fig. 7A<sub>3</sub>, A<sub>4</sub>); inflated parts of right valve consist of high angle irregular complex crossed foliated (Fig. 7A<sub>4</sub>).

*Remarks.*—The species *Pycnogryphaea weberae* was for the first time described by Yanin in the book by Tschelzova

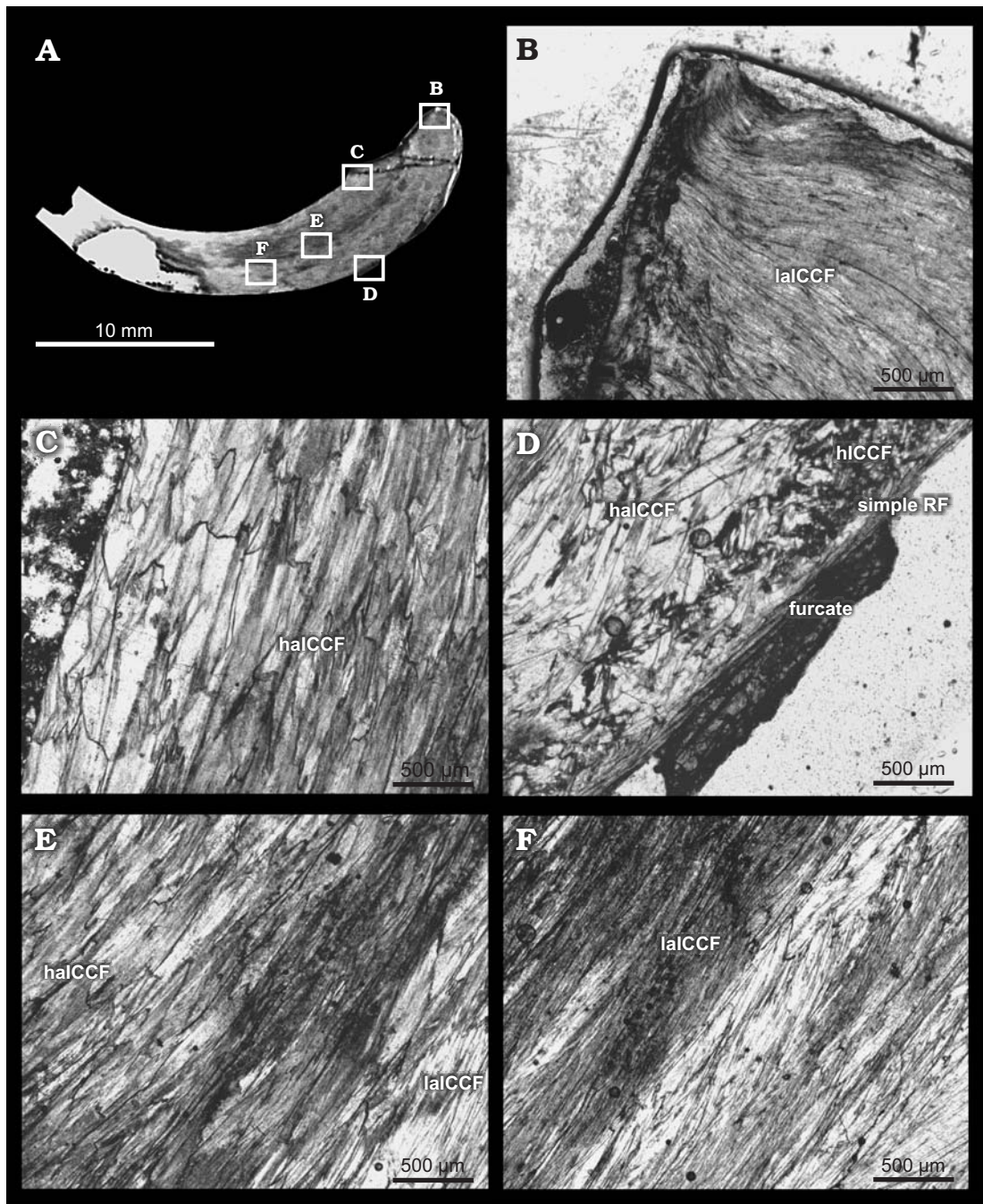


Fig. 6. Shell microstructure of pycnodontin oyster *Pycnogryphaea weberae* (Yanin in Tschelzova, 1969) from Berriasian of Crimea, section Balki village, *Dalmasiceras tauricum* Subzone. Thin section K-151-29 of left valve TsSGM 2088/35 with locations of photomicrographs (A); umbonal region represented by laICCF (B); internal part represented by haICCF (C); external part: endostracum consists of “furcate” microstructure, simple regular foliated microstructure (simple RF), hICCF and haICCF (D); central part represented by laICCF and haICCF (E, F). haICCF, high angle irregular complex crossed foliated microstructure; laICCF, low angle complex crossed foliated microstructure; simple RF, simple regular foliated microstructure.

(1969), and was attributed to the genus *Gryphaea*. Tschelzova (1969) studied the microstructure of *Pycnogryphaea weberae* and showed that inner shell layer was defined by a regular foliated microstructure with rare empty chambers and subrhombic microstructure, which includes various types of irregular complex crossed foliated microstructure. Furcate microstructure was observed on the outer shell layer. Such microstructures are typical for the genus *Gryphaea*,

and the species was included into *Gryphaea* by Yanin (in Tschelzova 1969). The current study of microstructure of *Pycnogryphaea weberae* agrees with the original description of Tschelzova (1969) (Figs. 6, 7). The presence of chomata mentioned on its original description (Yanin in Tschelzova, 1969), later encouraged Tamara N. Bogdanova (Arkadiev et al. 1997) and Boris T. Yanin (Arkadiev et al. 2012) to assign this species to the genus *Pycnodonte*.

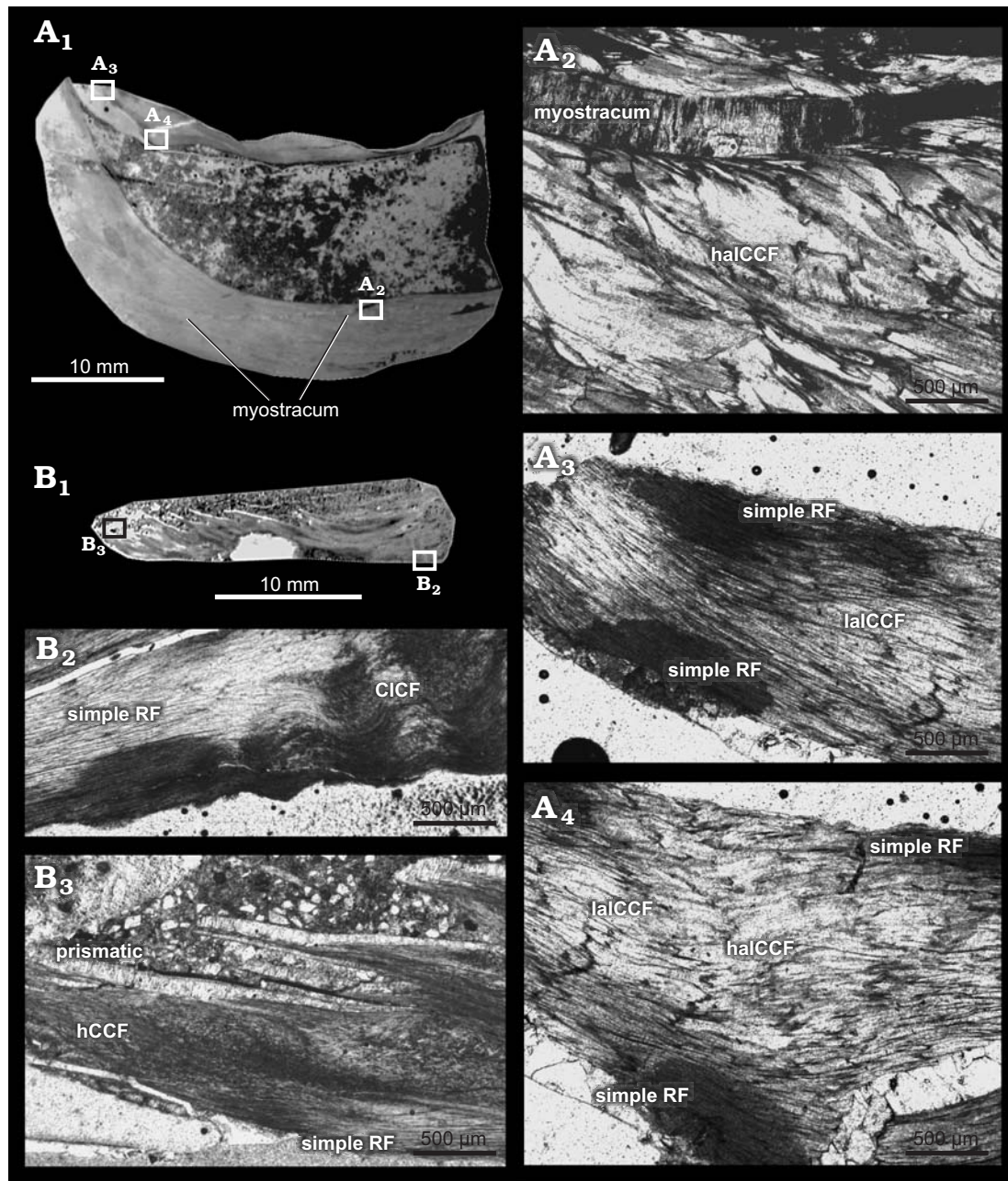


Fig. 7. Shell microstructure of pycnodontin oyster *Pycnogryphaea weberae* (Yanin in Tschelzova, 1969) from Berriasian of Crimea, section Balki village, *Dalmsiceras tauricum* Subzone. **A.** Thin section K-147-1 of left and right valves TsSGM 2088/36 with locations of photomicrographs (A<sub>1</sub>); inner part of left valve with myostracum consisting of irregular simple prismatic microstructure, microstructure of valve represented by haICCF (A<sub>2</sub>); umbonal part of right valve represented by simple RF and laICCF (A<sub>3</sub>); inner part of right valve represented by simple RF, laICCF and haICCF. **B.** Thin section K-151-10 of right valve with locations of photomicrographs (B<sub>1</sub>); umbonal part represented by simple RF and CICF (B<sub>2</sub>); outer part represented by hCCF and simple RF; exostracum consists of prismatic microstructure (B<sub>3</sub>). CICF, chomata-influenced crossed foliated microstructure; hCCF, homogeneous complex crossed foliated microstructure; haICCF, high angle irregular complex crossed foliated microstructure; laICCF, low angle complex crossed foliated microstructure; RF, regular foliated microstructure.

## Discussion

Stenzel (1971: N993–N994) noted: “All Pycnodontinae have chomata of a special character. In early, primitive genera of this subfamily (e.g., *Texigryphaea*), most species have low, narrow, short (1.5–2.0 mm), crowded ridgelets and corresponding grooves. On first inspection they are quite similar

to those found in many Ostreinae. However, they differ in that they are crowded (about 20 per cm) and set in series and in that the difference between the right and the left valves is obliterated, that is, the ridgelets cannot be distinguished from the pits because they are so crowded”. In the present work, the chomata observed on specimens of the species *Pycnogryphaea weberae* are characterized by a similar



structure. It agrees with the idea of Stenzel (1971) that early primitive Pycnodontinae are defined by simple chomata, whereas more advanced Pycnodontinae are characterized by the development of large vermiculate chomata near the hinge. No transitional Early Cretaceous oysters were found filling the gap between the true gryphaeas and pycnodontes, and Stenzel noticed (Stenzel 1971: N1077) that: "...certain traits seemingly foreshadow transitions to *Texigryphaea* and *Pycnodonte*. These traits are a broad and deep posterior sulcus dividing the left valve, an ill-defined smooth rounded radial keel running down the main body of the left valve, a slight amount of compression of the left valve in anteroposterior direction, a three-dimensional spiral growth pattern, a more opisthogyral left beak, and sharp radial grooves or gashes on the right valve". *Pycnogryphaea weberae* shares all of the mentioned morphological characters typical for Late Jurassic representatives of *Gryphaea* (*Bilobissa*). It differs from the Late Jurassic *Gryphaea* (*Bilobissa*) by the development of chomata (character of the Pycnodontinae). However, the species *Pycnodonte weberae* did not developed vesicular structure typical for most Pycnodontinae (with a single exception "*Pycnodonte*" *similis* (Pusch, 1837) characterized by reduced (but not absent) vesicular structure (Machalski 1988). Thus, *Pycnogryphaea weberae* may be regarded as a transitional taxon between Late Jurassic Gryphaeinae and Cretaceous Pycnodontinae. Comparisons made on shell morphology of *Gryphaea* (*Bilobissa*), *Pycnogryphaea* gen. nov., and *Phygraea* provide a basis for the reconstruction of phylogenetic line *Gryphaea* (*Bilobissa*) (Gryphaeinae; Late Jurassic) → *Pycnogryphaea* gen. nov. (Pycnodontinae; Berriasian) → *Phygraea* (Pycnodontinae; late Early Cretaceous).

*Pycnogryphaea* differs from *Gryphaea* by the appearance of chomata. Other morphological characters of *Pycnogryphaea* are typical for Gryphaeinae (circular posterodorsal adductor muscle scar, gryphaeoid shell shape, beaked umbo, posterior radial sulcus). The presence of chomata is a key morphological character that distinguished the Pycnodontinae from the Gryphaeinae. On the other hand, chomata (as also shell chambers) independently appeared several times during the evolution of Ostreoida in the subfamilies Exogyrinae Vialov, 1936, Pycnodontinae Stenzel, 1959, and Liostreinae Vialov, 1983 (Malchus 1998). However, other morphological characters of *Pycnogryphaea* are in common with Gryphaeinae and Pycnodontinae and there are no doubts that the genus belongs to Gryphaeinae–Pycnodontinae phylogenetic line.

The evolutionary trend from *Pycnogryphaea* gen. nov. to *Phygraea* includes the development of chambers filled by vesicular microstructure, increase of commissural shelf and the increase complexity from short simple chomata to long vermiculate chomata located only near the ligament area.

Finally, the Albian–Cenomanian genus *Texigryphaea* cannot be regarded as the earliest known Pycnodontinae and may be considered as a specialized member arising from the pycnodontes branch and restricted to North and Central America (Stenzel 1971).

The Late Jurassic genus *Circunula* Koppka, 2015, is defined by chomata and was consequently previously questionably included in the subfamily Pycnodontinae by Koppka (2015), but does not share morphological characters with the genera *Gryphaea* and *Phygraea*. Based on the present study, it cannot be regarded as an ancestor of the Pycnodontinae.

## Conclusions

*Pycnogryphaea* gen. nov. is proposed as a new genus within the subfamily Pycnodontinae. It includes the species *Pycnodonte weberae* (Yanin in Tschelzova, 1969) previously attributed to the genus *Pycnodonte* and is defined by well-developed short simple chomata and circumferential curb (characters of the Pycnodontinae), as well as a shell microstructure defined by irregularly complex crossed foliated and simple regularly foliated microstructures without chambering and vesicular structure (characters of the Gryphaeinae). The stratigraphic distribution of the subfamily Pycnodontinae is extended to the early Berriasian (*Berriasella jacobii* Zone). The combination of typical gryphaeine shell microstructure and pycnodontine morphology in the described specimens of the genus *Pycnogryphaea* suggest it may be considered as a transitional genus between both subfamilies, Gryphaeinae and Pycnodontinae.

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