

# On the systematics and phylogeny of the Triassic Pterinopectinidae (Bivalvia)

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A new classification of the Pterinopectinidae Newell, 1938 is proposed. It is based mainly on the structure of the ligament area. The family includes 3 subfamilies, 12 genera and 2 subgenera, among them subfamilies Pseudoclaraiinae and Claraiinae, and subgenus *Claraia* (*Bittnericlaraiia*) are new. The diagnoses and composition of all suprageneric taxa and the new subgenus are given.

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## Introduction

The paper deals mainly with the systematics of *Claraia* and *Claraia*-like bivalves. Among pterinopectinids they are guide fossils of the Lower Triassic, but still remain insufficiently studied. The Late Olenekian *Claraia* collected from Eastern Ciscaucasia and Mangyshlak will be described in a separate paper (Gavrilova, in press).

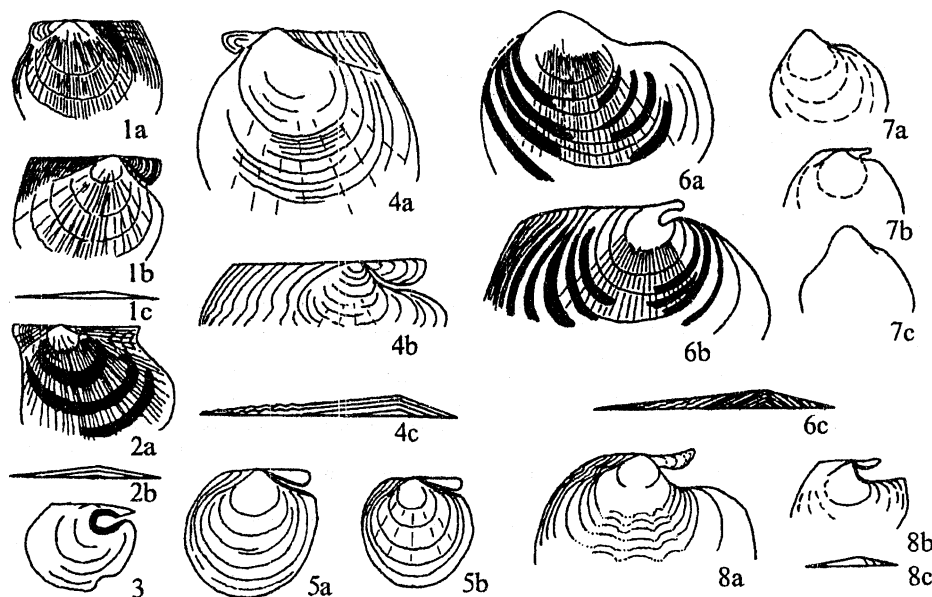
Bittner (1901) distinguished three subgenera within the genus *Pseudomonotis* Beyrich, 1862. This subdivision was based on the character of reduction of the hinge line of shells and their ornamentation. The most numerous group of species was assigned to the subgenus *Eumorphotis* with type species *P. (E.) telleri* (Bittner, 1901) (Werfenian Beds of Yugoslavia). It is noted for an intense evolution of auricles and a markedly variable shell ornamentation. The second subgenus, *Eumicrotis*, included the type species *P. (E.) hawni* Meek & Hayden, 1858 (Permian of Kansas) and a group of species with strongly reduced posterior auricles and ornamentation very similar to that of *Eumorphotis*. And, finally, the third group of species was distinguished as the subgenus *Claraia* Bittner, 1901, with the type species *P. (C.) clari* (Emmrich, 1844) from the Seiss Beds of the Southern Alps. This subgenus is characterized by the hinge line reduction, while the posterior auricle is far longer than the anterior one, and the concentric ornamentation dominates over the radial one.

In 1935, P. Leonardi upgraded *Claraia* to generic rank (cited from Zhang, 1980). He also presumed that *Claraia* existed from the Permian to the Early Triassic inclusive and originated from *Posidoniella*.

Ichikawa (1958) provided grounds for the separation of the genus *Claraia* and formulated the differences between the genera *Pseudomonotis* and *Claraia*. On the basis of revision of morphological features of shells and investigation of their ontogeny, he assigned *Claraia* to the subfamily Pseudomonotinae of the family Aviculopectinidae. He restricted the existence period of *Claraia* to the Early Triassic (Scythian). He also presumed that *Claraia* branched at end of the Permian from the genus *Limipecten*, from which pseudomonotids also branched off.

The systematic position of *Claraia* has long remained unstable due to the lack of information on the structure of the ligament area. It was placed in different families or subfamilies: (1) Aviculidae (Patte, 1935); (2) Aviculopectinidae, Aviculopectininae (Kulikov & Tkachuk, 1979; Moore, 1969); (3) Aviculopectinidae, Pseudomonotinae (Dickins & McTavish, 1963; Ichikawa, 1958); (4) Pseudomonotidae (Ciriacks, 1963; Ichikawa & Yin, 1966; Nakazawa, 1977, 1981); (5) Monotidae (Bychkov & al., 1976; Vozin & Tikhomirova, 1964) (6) Pectinidae (Li & Ding, 1981).

Since the publication of Zhang (1980), the structure of the ligament area of *Claraia* shells has been known. Zhang noted that the



Figs 1-8. Morphology of pterinopectinids: 1, *Dunbarella* Newell; 2, *Pterinopecten* Hall; 3, *Claraioides* Fang; 4, *Pseudoclaraiia* Zhang; 5, *Periclaraiia* Li & Ding; 6, *Claraia* (*Claraia*) Bittner; 7, *Claraia* (*Bittnericlaraiia* subgen. n.); 8, *Epiclaraiia* Gavrilova. 1a, 2a, 4a, 6a, 7a, 7c, left valve; 1b, 3, 4b, 5a, 5b, 6b, 7b, 8a, 8b, right valve; 1c, 2b, 4c, 6c, 8c, ligament area.

ligament of *Claraia* belongs to the duplivincular type. It is composed of both platy and fibrous material. The ligament area is narrow and long; it has the shape of a low elongated triangle and is characterized by the presence of  $\lambda$ -shaped complete and incomplete chevron grooves. Resilifer is lacking. On the basis of these features showing the ancient pectinoid type of the ligament area structure in *Claraia* shells, this genus was assigned to the family Pterinopectinidae. Study of the ontogeny of the ligamentary apparatus structure in various species of *Claraia* has demonstrated that with shell growth the ligament area becomes elongated, the arrangement of chevron grooves becomes denser and their number increases; in the adult stage, they are elongated lengthwise and become sinuous in the posterior part of the shell. Terminal shells display 4-5 asymmetric  $\lambda$ -shaped complete chevron grooves. The incomplete chevron grooves are distributed in such a way that in the anterior part of the shell there are 5 chevron grooves and in the posterior part their number reaches 20.

Using material from the Lower Triassic of Southern China, Zhang also distinguished the genus *Pseudoclaraiia* (Figs 4a-c, 10). The

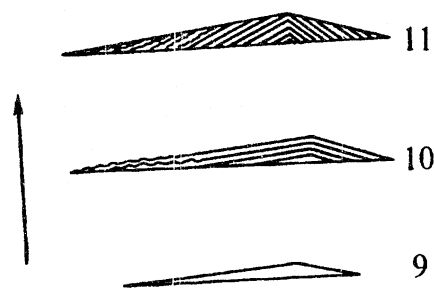
study of its morphological features revealed many features in common, reflecting affinities not only with *Claraia*, but also with the Carboniferous genus *Dunbarella* of the family Pterinopectinidae. Among the common features, the Chinese paleontologist listed the prosocline and inequivalve shell with the left valve being more convex than the right one, with the ligamentary apparatus without a hinge and resilifer, but with  $\lambda$ -shaped chevron grooves and with a prismatic layer having an irregular subsquare section. The characters distinguishing *Dunbarella*, *Pseudoclaraiia* and *Claraia* are the shape of the right anterior auricle and the peculiarities of the byssal notch. In addition, the first genus differs from the two others in the intercalation of radial costae on the left valve and bifurcation of ribbing on the right one, as well as in the presence of a radial ornamentation on auricles (Newell, 1938). In addition, comparison of the features of the ligamentary apparatus in these genera has revealed that the ligament areas were evolving from simple to complicated ones. *Pseudoclaraiia* and *Claraia* in the juvenile stage have retained the primitive structure of the area typical of *Dunbarella* (Figs 1a-b, 9). The analysis of changes of the morphological features in

time enabled Zhang to propose the scheme of phylogenetic affinities of the genera *Pterinopecten* – *Dunbarella* – *Claraia*.

Li & Ding (1981) established the genus *Periclaraia* with the type species *P. circularis* from the upper part of the Olenekian in the Anhui Province (China). These authors justly pointed to the similarity of the new genus with *Claraia* and *Dunbarella* in the shell shape and ornamentation. Among the features distinguishing *Periclaraia* from *Claraia* are the distinctly outlined, arcuately rounded left anterior auricle and undeveloped or indistinctly separated posterior auricles, and deep and narrow byssal notch obliquely directed upwards, towards the umbo. *Periclaraia* differs from *Dunbarella* in the rounded posterior dorsal margin of the shell, subrectangular byssal auricle, and weak and sparse simple radial ribbing or its absence in the middle part of the valve surface. Besides, unlike both genera mentioned, the genus *Periclaraia* is characterized by the presence of a ctenolium. Due to the poor knowledge of the structure of the ligament area, the genus *Periclaraia* was conditionally assigned to the family Pectinidae.

Presumably, *Periclaraia*, in its shape, extent of inequivalvity and variability of the hinge line length is closer to the genus *Pseudoclaraiia*. However, it differs from the latter in the less sloping or straight shell with eccentric umbos, outline of auricles (an arcuate left anterior auricle and a longer, subrectangular byssal auricle rounded in the anterior part), wedge-shaped notch obliquely directed towards the umbo and the presence of a ctenolium (Figs 5a, 5b). On the basis of the revealed features, the genus *Periclaraia*, with a certain conditionality, may be assigned to the family Pterinopectinidae. The genus *Periclaraia* has been found in association with ammonoids *Pseudoceltites* sp., *Hellenites* sp., *Subcolumbites* sp., *Columbites costatus* Chao, C. sp., *Tirolites* cf. *spinosus* Mojs., T. sp. (Li & Ding, 1981, p. 326). The stratigraphic range of the latter can be correlated with Zones cassianus and parisianus of the Upper Olenekian substage of the Tethyan standard.

Genus *Claraioides* with the type species *C. primitivus* Yin, 1982 from the Upper Permian (Changxinian) of Southern China was distinguished by Fang (1993). On the basis of the morphological similarity with *Pseudoclaraiia* and *Claraia*, Fang assigned *Claraioides* to the family Pterinopectinidae. The characteristic features of the above genus



Figs 9–11. Pterinopectinidae, chevron grooves, showing morphogenesis of ligament area: 9, *Dunbarella* Newell; 10, *Pseudoclaraiia* Zhang; 11, *Claraia* Bittner.

are: the elliptical outline of the shell; the narrow and elongated byssal auricle with narrowing margin, its size being much greater than that of the left anterior auricle; the deeply incised subrounded (bay-like) byssal notch surrounded by a thickened rim, due to which *Claraioides* is easily discernible from the genera *Claraia* and *Pseudoclaraiia* (Fig. 3). Besides, the genus *Claraioides*, unlike the latter, has a ligament area with 1–2  $\lambda$ -shaped complete grooves (Fig. 2b).

Comparison of the specific features of the near-umbo part of the right valves of *Claraioides*, *Pseudoclaraiia* and *Claraia* enabled Fang to presume that the representatives of these genera were attached epibenthic organisms. An attached mode of life was ensured by the stabilization mechanism in the form of a byssal notch. Fang (1993, p. 657) proposed three possible versions of phylogenetic affinities between genera within the family Pterinopectinidae. We presume that the first version, in which the origin of *Claraia* from *Pseudoclaraiia*, and not from *Claraioides* is accepted, is the most probable. The last-mentioned genus has a more primitive ligament area with 1–2 pairs of  $\lambda$ -shaped complete chevron grooves, similar to the Devonian genus *Pterinopecten* (Figs 2a, b). The Carboniferous genus *Dunbarella* (Figs 1a, b) has a similar structure of the area, but with a single chevron groove.

Therefore, I propose to subdivide the family Pterinopectinidae into three subfamilies: Pterinopectininae, Pseudoclaraiinae subfam. n. and Claraiinae subfam. n. This subdivision is based on the differences in the structure of the ligament area. The nominotypical subfamily comprises the genera with a primitive type of ligament. The ligament area is composed of 1–2  $\lambda$ -shaped complete chevron grooves retaining at all stages of the ontogeny a rectilinear shape in the anterior and

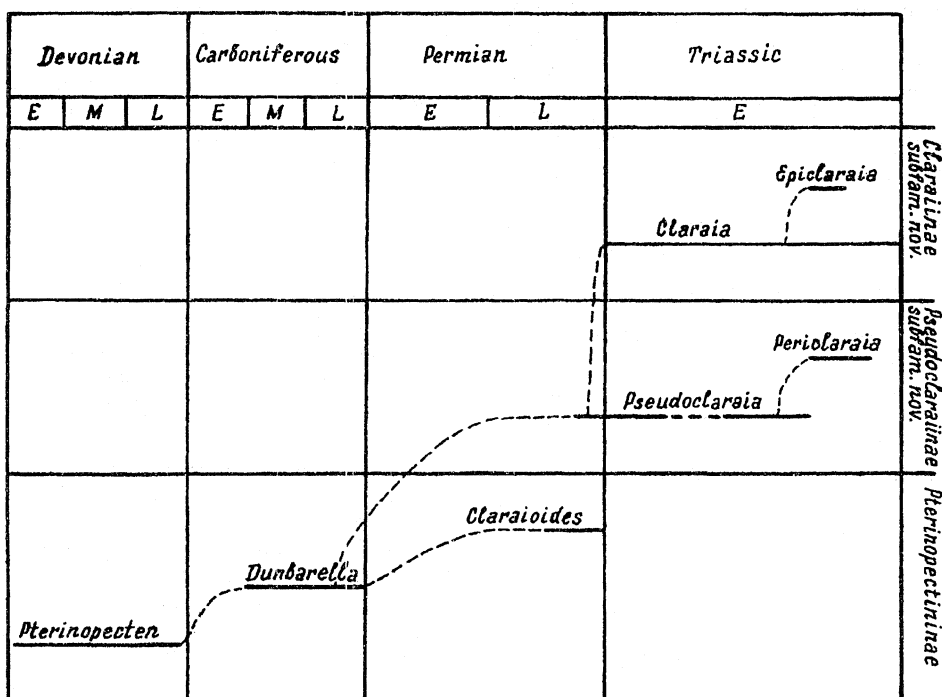


Fig. 12. Phylogenetic relationships within Pterinopectinidae.

posterior parts of the shell (Figs 1c, 2b, 9). The subfamily Pseudoclaraiinae comprises the genera with the ligamentary apparatus with more than two pairs of  $\lambda$ -shaped complete chevron grooves. With the shell growth, the latter become elongated lengthwise and take a sinuous shape in the posterior part of the shell (Figs 4c, 10). The subfamily Claraiinae comprises the genera with composite structure of the area. It is composed of 4-5 asymmetric  $\lambda$ -shaped complete and 20-25 incomplete chevron grooves. The latter are distributed in such a way, that in the anterior part of the terminal shells there are 5 chevron grooves and in the posterior part their number reaches twenty. They are extended lengthwise and take a sinuous shape in the posterior part of the shell (Figs 6c, 11).

The analysis of the morphological features of pterinopectinid shells enables to assess their diagnostic significance. Thus, the structure and type of the ligament apparatus, the structure of the prismatic layer, the prosocline and inequivalve character of the shell appear to be most useful for the diagnostic of families. The number, form and character of changes in chevron grooves and growth of the shell make it possible to distinguish the

subfamilies. The most valuable features for the taxonomy of the genera are the evolution degree of auricles and the shell outline. The ratio of the shell length to its height, the degree of inequivalvity, development degree and eccentricity of umbos and the peculiarities of ornamentation can be used to distinguish subgenera.

The family Pterinopectinidae includes three subfamilies, 12 genera and 2 subgenera. The composition of the nominotypical subfamily is determined more precisely. Special emphasis is placed on the generic composition of the new subfamilies. Pseudoclaraiinae comprises the genera *Pseudoclararaia* Zhang, 1980 and *Periclararaia* Li & Ding, 1981. The genera *Claraia* Bittner, 1901 and *Epiclararaia* Gavrilova, 1995 are considered within Claraiinae. The genus *Claraia* is subdivided into subgenera *Claraia* Bittner, 1901 and *Bittnericlararaia* subgen. n.

Family **PTERINOPECTINIDAE** Newell, 1938

*Diagnosis.* Prosocline or acline pectinoids with posterior auricles longer than anterior, poorly or well differentiated; inequivalve,

right valve less convex than left one; hinge edentulous; ligament area narrow, without resilifers but bearing a series of asymmetrical  $\lambda$ -shaped complete chevron grooves (extending the length of the area, with apex below beaks) or incomplete ones (extending only before or behind beaks); ligament duplivincular; outer ostracum of right valve prismatic with irregular subsquare section.

Subfamily PTERINOPECTININAE Newell, 1938

Type genus *Pterinopecten* Hall, 1883.

**Diagnosis.** Ligament area with one or two pairs of  $\lambda$ -shaped complete chevron grooves retaining at all stages of ontogeny rectilinear shape in anterior and posterior parts of shell.

**Composition.** *Pterinopecten* Hall, 1883, U. Silurian – U. Devonian; *Anulipecten* Ruzicka, Prantl & Pribyl, 1959, U. Devonian; *Dunbarella* Newell, 1938, Carboniferous (Mississippian, Pennsylvanian); *Limanomia* Gray, 1850, U. Devonian (Frasnian); *Lyriopecten* Hall in S.A. Miller, 1877, M. – U. Devonian; *Pseudaviculopecten* Newell, 1938, M. Devonian – L. Carboniferous (L. Mississippian); *Pterinopectinella* Newell, 1938, U. Mississippian – L. Permian (Leonard); *Claraia* Fang, 1993, U. Permian (Changxingian – Wuchiapingian).

**Remarks.** This subfamily is distinguished from the other subfamilies of Pterinopectinidae by smaller number of  $\lambda$ -shaped complete chevron grooves retaining rectilinear shape in the anterior and posterior parts of the shell at all stages of ontogeny. It differs from the subfamily Claraiinae in the absence of incomplete chevron grooves.

Subfamily PSEUDOCLARAIINAE subfam. n.

Type genus *Pseudoclaraiia* Zhang, 1980.

**Diagnosis.** Ligament area with more than two pairs of  $\lambda$ -shaped complete chevron grooves elongated lengthwise and becoming sinuous in posterior part of adult shell.

**Composition.** *Pseudoclaraiia* Zhang, 1980, U. Permian (Changxingian) – L. Triassic (Induan – L. Olenekian) and *Periclaraiia* Li & Ding, 1981, L. Triassic (U. Olenekian).

**Remarks.** This subfamily differs from the nominotypical subfamily in the more numerous  $\lambda$ -shaped chevron grooves elongated lengthwise and becoming sinuous in the posterior part of the adult shell; from Claraiinae

it differs in the absence of incomplete chevron grooves.

Subfamily CLARAIINAE subfam. n.

Type genus *Claraia* Bittner, 1901.

**Diagnosis.** Ligament area with numerous chevron grooves (4-5  $\lambda$ -shaped complete and 20-25 incomplete) elongated lengthwise and becoming sinuous in posterior part of adult shell.

**Composition.** *Claraia* Bittner, 1901, L. Triassic; *Epiclaraiia* Gavrilova, 1995, L. Triassic (U. Olenekian).

**Remarks.** This subfamily is distinguished from the other Pterinopectinidae subfamilies by the presence of incomplete chevron grooves. In addition it differs from the nominotypical subfamily in the complicated structure of ligament area. The latter bears numerous chevron grooves (complete and incomplete), elongated lengthwise and becoming sinuous in the posterior part of the adult shell. I include the genus *Epiclaraiia* in this subfamily for the presence of a few incomplete chevron grooves only in anterior part of its hinge line (Gavrilova, 1995) (Fig. 8c).

Genus *Claraia* Bittner, 1901

Subgenus *Bittnericlaraiia* subgen. n.

Type species *Pseudomonotis decidens* Bittner, 1899.

**Diagnosis.** Shell length less than height. Left valves varying from strongly convex to inflated with very prominent umbo above the hinge line; beak massive, orthogyre, rarely prosogyre, nearly central (lying between anterior third and middle of shell), surface smooth or covered with weak closely-set growth lines; right valve much less convex than left.

**Composition.** *Claraia* (*Bittnericlaraiia*) *painkhandana* (Bittner, 1899) (L. Induan: Zone woodwardi of the Central Himalayas, Zone tibeticum of Southern China), *C. (B.) decidens* (Bittner, 1899) (L. Olenekian, Zones gracilitatis and pluriformis of the Central Himalayas, Kashmir), *C. (B.) punjabiensis* (Wittenburg, 1909) (L. Olenekian, Zones gracilitatis and pluriformis of the Salt Range), *C. (B.) australasiatica* (Krumbeck, 1924) (L. Olenekian, Zones gracilitatis and pluriformis of the Primorsk Territory and Timor), *C. (B.) australasiatica kumschokensis* Gavrilova, in press (U. Olenekian, Zone cassianus of Mangyshlak).

**Remarks.** This subgenus differs from the nominotypical one in the tall outline of the shell with more developed prosogyral beak, presence of moderate convexity of right valve and smooth surface. All species of the new subgenus were attributed formerly to the species group *Claraia decidens* (Ichikawa, 1958; Nakazawa, 1977).

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