MIDDLE CAMBRIAN PELECYPODS FROM THE ANTI-ATLAS, MOROCCO

Gerd Geyer¹ and Michael Streng²

E-mail: gerd.geyer@mail.uni-wuerzburg.de
² FB-5 Geowissenschaften. Universität Bremen. P. O. Box 330 440. D-28334 Bremen. Germany. E-mail: streng@uni-bremen.de


ABSTRACT

A new species of the Early to Middle Cambrian pelecypod genus Pojetaia is reported from the early Middle Cambrian of the Moroccan Anti-Atlas with the new species Pojetaia sarhoensis. Arhouriella opehodontoides n. gen. and sp. is the first report of a Cambrian pelecypod with an amphidetic, slightly twisted and partly internal ligament and appears to represent a second order of pelecypods in the early Middle Cambrian. Preservation, environment and correlation are discussed. Species of Pojetaia are discussed in detail. Jellia is shown to be a junior synonym of Pojetaia. Hence, the species originally described under the names P. runnegari and Jellia ovata by Li and Zhou (1986) need to be renamed. Oryzocochla He and Pei, 1985 is regarded as an invalid taxon. Other Cambrian pelecypods are reviewed briefly.

Key words: Pojetaia sarhoensis n. sp., Arhouriellidae n. fam., Arhouriella opehodontoides n. gen., n. sp., Pelecypoda, morphology, synonymy, phylogeny, preservation, Middle Cambrian, Morocco, China, Australia.

RESUMEN

Se define Pojetaia sarhoensis, una nueva especie del género de pelecípodo Pojetaia del Cámbrico Inferior-Cámbrico Medio, procedente del Cámbrico Medio temprano del Anti-Atlas, Marruecos. Se define también Arhouriella opehodontoides n. gen. and sp., que es el primer bivalvo cámbrico descrito con ligamento anfibéctico ligeramente retorcido y parcialmente interno, por lo que parece representar un segundo orden de pelecípodos en el Cámbrico Medio temprano. Se discute la conservación, el medio de vida y la correlación de este material. Se discuten también, en detalle, las especies de Pojetaia. Jellia se considera un sinónimo más reciente de Pojetaia. Por lo tanto, el material descrito por Li y Zhou (1986) bajo los nombres P. runnegari y Jellia ovata debe ser renombrado. Oryzocochla He y Pei, 1985 resulta ser un taxón no válido. Se revisan brevemente otros pelecípodos cámbricos.

Palabras clave: Pojetaia sarhoensis n. sp., Arhouriellidae n. fam., Arhouriella opehodontoides n. gen., n. sp., Pelecypoda, morfología, sinonimia, filogenia, conservación, Cámbrico Medio, Marruecos, China, Australia.

INTRODUCTION

Pelecypods are rare in Cambrian biota. The specimens described herein are the first Middle Cambrian pelecypods from western Gondwana and the first pelecypods from the present-day continent Africa.

The only other western Gondwanan Cambrian pelecypods were reported from Lower Cambrian rocks of the Görlitz area, eastern Germany (Elicki, 1994). Fossils that were originally interpreted as the earliest known pelecypods were described from the Iberian Chains, northeastern Spain under the name Lamellocosta simplex (Vogel, 1962, 1975). However, these remains turned out to be distorted valves of the obolellid brachiopod

**LOCALITY, AGE, AND ENVIRONMENT**

The specimens all come from sample horizon JAR-0.56 of the Jbel Arhouri section, about 5 km south of Timatraouine on the southern slope of Jbel Arhouri (Lambert coordinates 472/487, on the Dadès map sheet: Fig. 1). The section is probably identical with the locality first discovered by J. Hindermeyer in 1954. Stratigraphic data from this section were used by Hupé (1959) for his Timatraouine section (section 44 in Hupé, 1959). The section was earlier described in detail by Geyer et al. (1995).

The base of the section nonconformably overlies a late Precambrian granitoid complex. The late Precambrian basement in this area was exposed to erosion prior to the lower Middle Cambrian *Cephalopyge notabilis* Zone. The Middle Cambrian transgression flooded the Jbel Arhouri area during the *Cephalopyge notabilis* Chron and inundated a granitoid complex creating lithologies that change rapidly laterally (Fig. 2). The basal conglomerates and coarse sandstones are overgrown by laminar and columnar LLH-type stromatolites. Locally, oncocoids may rest on the basal laminar algal mats, and columnar stromatolites arise from these oncocoidal layers. The space between the columnar stromatolites is filled with reworked debris of shelly fossils, such as trilobites, obolellid and acrotretid brachiopods, echinoderms and numerous small shelly fossils such as helcionellids, pelagiellids and hyoliths. Remarkably, these fossil groups are relatively diverse and contain a number of fossils that are rarely found or even unknown from other localities.

The limestone bed and overlying monotonous fine-grained sandstones with intercalated limestone layers represent the Brèche à Micmacca Member of the Jbel Wawrmast Formation, Feijas internes Group (Geyer, 1989, 1990a, 1990c). The stratigraphic concept of this member was derived from a limestone layer exposed near Ourika Wawrmas, north-central Anti-Atlas (compare Geyer and Landing, 1995). Fossil debris, oncocoids, and stromatolites represent a shallow marine, high energy nearshore to shoreface environment.

The *Pojetaia* specimens described herein come from these assemblages. Samples were taken from fossil hash limestones intercalated between stromatolites at the top of the LLH-type stromatolitic limestones and from the overlying centimeters of fossil hash limestones over a distance of several meters in lateral extension (Fig. 3). Trilobites from the assemblages clearly indicate the early Middle Cambrian *Cephalopyge notabilis* Biozone (Geyer, 1990b). The *Cephalopyge* Zone is a representative of the *Acinetopus/Acidiscus* assemblage (Robison et al., 1977;
Figure 2. Schematic overview of the sequence boundary at the base of the Jbel Arhouri section. The obliquely truncated granitic basement is pierced by Hercynian aplite dikes that caused local thermal metamorphism. Conglomerates and local overlying coarse-grained sandstones (small stipple) end at an erosional surface that is capped by stromatolitic-shelly limestones (horizontal hachures) with primarily low cyano bacterial mats. Oncoidal and oolithic lenses, as well as columnar LHH- or SH-V-type stromatolites, overgrow this layer and suggest a second stage of deposition. (After Geyer et al., 1995: fig. 22.)

Geyer (1990b, d) which is commonly regarded as late Early Cambrian in age, and its faunas have been compared with faunal associations of other realms, such as those of the protolenid interval (“Protoelenus zone”) of Comley, Shropshire, the Acidiscus theristis and Bathyscius taconicus “subzones” of southeastern Newfoundland (Fletcher, 1972; Landing, 1992), and less clearly with the faunas of the upper Toyonian Stage of Siberia (Geyer, 1990d). Correlata of the Cephalolyge Zone into Laurentia is a matter of uncertainty at present, owing to strong faunal provinciality. Further discussion on the stratigraphy is detailed in Geyer (1993), Geyer and Palmer (1995), and Geyer (1998).

PRESERVATION

The limestone beds of the Brèche à Micmacca Member are generally limonitic-rich sparry wackestones and packstones so that fossils with primarily calcitic or argonitic shells are commonly preserved as limonitic internal and external molds, or their shells are replaced by limonitic substances. Accordingly, most specimens of Pojetaia sarhoensis n. sp. from JAR-0.56 are limonitic internal molds, often with parts of the external limonitic coat adhering at the infillings of gaping shell margins. Rarely, steinkerns of Pojetaia sarhoensis may partly be phosphatized. In those cases, only the internal molds are preserved. External coats of the shell most probably attained only minor thicknesses that were unsuitable for preservation during dissolution with formic acid.

Hercynian aplites, which are represented in the Jbel Arhouri section by dikes that pierced the brittle granitoids (Fig. 2), did not intrude the more ductile, Middle Cambrian, fine-grained sandstones. However, they created local metamorphism and partly transformed the basal Middle Cambrian conglomerates and limestones. The basal limestones are partly transformed into structureless marbles, and the carbonate was replaced by silica that preserved most of the structures. The bivalves from JAR-0.56 are thus preserved in part as silicified shells.

SYSTEMATIC PALEONTOLOGY

Specimens examined in this study were obtained by etching of rock samples in dilute formic acid. Limonitic and occasionally phosphatized steinkerns as well as silicified shells were picked from the remaining insoluble residues.

The material is deposited in the collection of the Institut für Paläontologie der Universität Würzburg (PIW), Würzburg (Germany).

CLASS PELECYPODA Goldfuss, 1820

The record of Cambrian pelecypods includes:
- Fordilla Barrande, 1881, with F. troyensisis Barrande, 1881, from the Early Cambrian of the Taconic slice in the New York State (U.S.A.), of Newfoundland, Greenland, Germany, and Bornholm (Denmark), F. sibirica Krasilova, 1977, from the Tommotian of the Siberian Platform, and F. germanica Elicki, 1994, from the Early Cambrian of the Görlitz area (eastern Germany);
- Pojetaia Jell, 1980, with Pojetaia runnegari Jell, 1980 from the Cambrian of South Australia and western New South Wales (additional material described as P. runnegari from Anhui Province, China, and from Germany is discussed below), P. ovata Chen and Wang, 1985 from the Early Cambrian of Henan Province, P.
**Figure 4.** *Pojetaia sarhoensis* n. sp. All from Jebel Arhouri section, sample horizon JAR-0.56. • A. Paratype, PIW 1997IV24. Detail of internal mold showing posterior hinge area and filling of opisthobetic ligament slot with faint growth lines (arrow). (x150.) • B. Paratype, PIW 1997IV11. Lateral view of limonitized left valve with partially preserved shell structure. (x100.) Note concentric growth lines on external surface and faint radial striae (arrow) that probably sketch aragonitic fibres in the external shell layer of the shell. Corroded areas show crystallite bundles arranged obliquely to the horizontal and radial axes of the shell which indicate irregular prismatic layer. • C. Paratype, PIW 1997IV4. Oblique dorsal view of internal mold with infillings of sockets corresponding to four hinge teeth. (x75.) • D. Paratype, PIW 1997IV21. Left lateral view partly exfoliated specimen showing supposed pallial line/pallial attachment. (x50.) • E. Paratype, PIW 1997IV18. Internal mold, lateral view of hinge with imprints of four hinge teeth. (x75.) • F. Paratype, PIW 1997IV11. Detail of umbonal area with faint concentric growth lines, radial striae and crystallite bundle at corroded umbo. (x150).

*elliptica* Li and Zhou, 1986 from the Early Cambrian of Anhui Province, both North China Platform, *Pojetaia osiseensis* Hinz-Schalbreuter, 1995 from the Middle Cambrian of Bornholm, and *Pojetaia* sp. from the Early Cambrian of Bornholm, Denmark (Berg-Madsen, 1987);  
- *Buliniella* Yermak, 1986 from the Early Cambrian of the Siberian Platform;  
- *Tuarangia* MacKinnon, 1982, with *T. paparua* MacKinnon, 1982, from the late Middle Cambrian of New Zealand, *T. gravgaardensis* Berg-Madsen, 1987 and *T. gravgaardensis tenuiumbonata* Hinz-Schalbreuter, 1995, both from the late Middle Cambrian of Bornholm (Denmark), and *Tuarangia* sp. from an erratic boulder of probable early Late Cambrian age of western Pomerania, Poland (Berg-Madsen, 1987);  
- *Oryzococcha* He and Pei, 1985, with *O. prisca* He and Pei, 1985 from the Early Cambrian of Henan Province, North China Platform;  
- *Canyia* Hinz-Schalbreuter, 1995 from the late Middle Cambrian of Bornholm, Baltica.

Some of these forms are interpreted as representatives of other fossil groups or as junior synonyms, but it remains especially remarkable and a puzzling fact that no undisputed pelecypods are known from Upper Cambrian strata. For discussion of synonymy under *Pojetaia* see Discussion under *Pojetaia sarhoensis* n. sp. below.
assigned to X. elliptica has blade-like structures such as the material described from Hubei. These structures are interpreted as teeth. However, it remains doubtful whether the Guizhou material is congeneric or even conspecific with X. elliptica as described by Zhang (1980). Both X. elliptica (known from a single specimen) and X. elongata (known from three slightly to considerably distorted specimens) have a pelecypod-type habit, but are inadequately preserved for systematic determination.

Tuarangia MacKinnon, 1982 has been interpreted as a bivalved “monoplacophoran” rather than a pelecypod (Runnegar, 1983; Runnegar and Pojeta, 1985). Although Tuarangia is a striking analogy of the “quasirostroconch” Pseudomyoniana Runnegar, 1983, morphological details that support this interpretation remain equivocal, and more material of further related taxa is needed to give evidence for either interpretation.

Camya Hinz-Schallreuter, 1995 is known only from the type material, two strongly inequilateral left and possibly juvenile valves, that do not show any clear dentition.

The species of Fordilla range from the early late Early Cambrian to the late late Early Cambrian (probable equivalents of the Siberian Atadabanian and Botoman); Pajetaia was previously known from the upper Tommotian to the earliest Middle Cambrian in Australia (probable equivalents of the Siberian upper Toyonian) and is now also known (this paper) from probable equivalents of the Siberian upper Toyonian in Morocco.

SUBCLASS PALAEOTAXODONTA Korobkov, 1954

ORDER NUCULOIDA Dall, 1889

Family Praenuculidae McAlester, 1969

The family Praenuculidae includes Early Cambrian through Devonian nuculoids with a simple, external ligament. Fordilla and Pajetaia resemble juvenile individuals of more advanced praenuculids so that they can be accommodated in this family although their characters are few and relatively insignificant.

Pajetaia Jell, 1980

Type species: Pajetaia runnegari Jell, 1980, p. 235 (by original designation).

Discussion

Despite the general paucity of Cambrian pelecypods, Pajetaia is a widespread genus, now known from Australia, China, Morocco, Germany, and Denmark. Although the characters are limited in number, they permit identification of a number of species with limited geographic ranges. Examination of published species suggests modification of the nomenclature of several forms.

Pajetaia ovata Chen and Wang, 1985 was described from the Early Cambrian of Henan, on the North China
Figure 6. Relations of dimensions in *Pojetaia sarhroensis* n. sp. • A. Total length vs. height. • B. Length vs. width. • C. Total length vs. anterior length. • D. Total length vs. ratio anterior length/total length. (All values in µm.) See figure 5 for location of measurements. Explanations in the text.

Platform. Specimens from the same and nearby localities were described as *Pojetaia runnegari* by He and Pei, 1985, but represent the same distinct species.

Li and Zhou (1986) described two genera and four species of pelecypods from the Lower Cambrian Yutaishan Formation of Anhui on the North China Platform, under the names *Pojetaia runnegari* Jell, 1980, *P. elliptica* Li and Zhou, 1986, *Jellia elliptica* Li and Zhou, 1986, and *J. ovata* Li and Zhou, 1986. The authors refused the interpretation of a common transposition of the teeth, and their new genus *Jellia* Li and Zhou, 1986 is based on forms with a "main tooth" on the right valve, whereas the concept of *Pojetaia* is reduced to only include forms with the "main tooth" on the left valve. The two species found for *Pojetaia* and *Jellia* are thus morphological counterparts placed into two different genera. However, we interpret these pairs of species as representatives of a single species each with frequently transposed hinge. This interpretation follows that for *Fordilla* and *Pojetaia* by Krasilova (1977), Jell (1980), and Runnegar and Bentley (1983). Transposition was apparently a common feature in the Cambrian pelecypods, but is a character that is occasionally observed in post-Cambrian and even recent pelecypods. Thus, *Jellia elliptica* is a synonym of *Pojetaia elliptica*, and *Jellia ovata* is a synonym of *Pojetaia runnegari* of Li and Zhou (1986). Both species are distinguished by 1) the shape of the valves which is more subelliptical in *P. elliptica* and more oval in their *P. runnegari*, and by 2) the auricle which is better developed in their *P. runnegari*

and thus creates a smaller angle in lateral view (130-135° in their Chinese *P. runnegari* in contrast to 120-130° in *P. elliptica*).

*Pojetaia runnegari* of Li and Zhou (1986) differs from the type material of *P. runnegari* in having a larger posterodorsal angle of the auricle and less projecting umbones on internal molds; it represents a different species. For this species, the name *Jellia ovata* Li and Zhou, 1986, would be available. However, *P. ovata* (Li and Zhou, 1986) is a junior homonym of *P. ovata* Chen and Wang, 1985. Therefore a new name needs to be chosen.

*Fordilla germanica* Elicki, 1994 differs from *F. troyensis* Barrande, 1881 and *F. sibirica* Krasilova, 1977 in having an elongate rather than oval lateral outline, subcentral umbones, and a small posterodorsal auricle. These characters suggest that the species is better placed in *Pojetaia*.

*Oryzoconcha* He and Pei, 1985 (type species, *O. prisca* He and Pei, 1985), from the Early Cambrian of Henan, North China Platform, is based on imperfectly preserved material and on specimens with characters of *Pojetaia* and is thus a junior synonym of *Pojetaia* as suggested earlier by Runnegar (in Berg-Madsen, 1987).

*Pojetaia sarhroensis* n. sp.

Figs. 4-6; Pl. I

**Holotype:** PIW 1997IV25 (Pl. I, fig. 12). **Paratypes:** 49 internal molds with or without partial limonitic coats,
Table I. Comparison of distinctive characters in the species of Pojetaia. Explanation in the text.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>REFERENCE</th>
<th>OCCURENCE</th>
<th>SHAPE</th>
<th>BEAKS ON STEINKERN</th>
<th>AURICLE ANGLE</th>
<th>DENTITION</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. runnegari</em></td>
<td>Jell, 1980</td>
<td>southern Australia</td>
<td>oval</td>
<td>prominent</td>
<td>110-120°</td>
<td>2 hinge teeth</td>
</tr>
<tr>
<td><em>P. ovata</em></td>
<td>Chen &amp; Wang, 1985</td>
<td>Henan Province, North China Platform</td>
<td>oval</td>
<td>short</td>
<td>110-120°</td>
<td>2-3 hinge teeth, middle tooth largest</td>
</tr>
<tr>
<td><em>P. elliptica</em></td>
<td>Li &amp; Zhou, 1986</td>
<td>Anhui Province, North China Platform</td>
<td>elliptical</td>
<td>short</td>
<td>120-130°</td>
<td>2-3 hinge teeth, middle tooth largest</td>
</tr>
<tr>
<td>&quot;J.&quot; elliptica</td>
<td>Li &amp; Zhou, 1986</td>
<td>Anhui Province, North China Platform</td>
<td>oval</td>
<td>short</td>
<td>130-135°</td>
<td>2-3 hinge teeth, middle tooth largest</td>
</tr>
<tr>
<td><em>P. germantica</em></td>
<td>Elicki, 1994</td>
<td>Germany, western Gondwana</td>
<td>elliptical</td>
<td>short</td>
<td>120-130°</td>
<td>unknown</td>
</tr>
<tr>
<td><em>P. sarthreensis</em></td>
<td>this study</td>
<td>Morocco, western Gondwana</td>
<td>oval</td>
<td>short</td>
<td>130-135°</td>
<td>2-3(4) hinge teeth, size tends to decrease anteriorly</td>
</tr>
<tr>
<td><em>P. osteoensis</em></td>
<td>Hinz-Schalreuter, 1995</td>
<td>Bornholm, Baltica</td>
<td>elliptical</td>
<td>short</td>
<td>ca. 135°</td>
<td>3 hinge teeth</td>
</tr>
</tbody>
</table>

Locus typicus: Jbel Arhouri section, east-central Anti-Atlas.

Stratum typicum: Sample horizon JAR-0.56, Jbel Warwasm Formation, Brèce à Micmacca Member; Cephalopyge notabilis Zone, early Middle Cambrian.

Derivatio nominis: Named after the Jbel Sarrhre area, east-central Anti-Atlas, Morocco, in which the type locality is located.

Diagnosis: Posterior auricle faintly marked and narrow. Dentition of (usually) sinistral valve of adult individuals with three teeth, anterior tooth minute.

Description
Shell equivalved, roughly equilateral. Valves of adult specimens venericform and oval, juvenile valves elongate. Umbones prosogyrate, beads near midlength, poorly projecting in internal molds. Posterior auricle faintly marked, includes posterior angle of approximately 130 to 135° in lateral view of adult valves.

Exterior of valves usually smooth or with faint growth lines, rarely with shallow, broad concentric ribs. Anterior sector sometimes defined by one or two shallow radial ribs. Very fine radial lines seen in PIW 1997IV11 (Fig. 4B, F) are due to corrosion and possibly mark junction of crystallite bundles with the external surface of the outer shell layer.

Interior of valves smooth, except for multiple-paired pedal muscle scars arranged in a position similar to a supposed pallial line/pallial attachment. Number of pallial muscle tracks vacillates from five to probably nine, with broader and less discrete imprints in the anterior part, and form a non-sinusuate trail (Pl. I, fgs. 5, 6, 8, 9; Fig. 4D).

Probable anterior adductor muscle scar relatively small, located at anterior end of pallial muscle tracks. Anterior pedal retractor muscle insertion is faintly indicated relatively close to the anterior end of the hinge in one of the specimens.

Dorsal margins of valves strengthened. Ligament opisthospheric, with almost half shell length, lenticular in dorsal view. Ligament areas elongate, straight, occasionally with growth lines (Fig. 4A, B).

Dentition consists of generally two to three peg-like teeth and corresponding sockets, occasionally with four sockets or teeth (Fig. 4C, E). A silicified left valve has a hinge plate that carries three stout and broad-based teeth which decrease in size posteriorly (Pl. I, figs. 1-3). Dentition sometimes transposed (compare Pl. I, fgs. 10 and 12).

Ontogeny and autecology
The studied material includes isolated valves and steinkerns that range from 680 to 2,250 μm in length and thus represent an ontogenetic series from immature through most probably gerontic individuals. Although the 50 sampled individuals are clearly less than those of *Pojetaia runnegari* studied by Runnegar and Bentley (1983), the size range clearly exceeds that reported from *Pojetaia runnegari* (0.7 to 1.6 mm; Runnegar and Bentley, 1983: 82). This indicates that the specimens may, at least partly, represent populations composed of individuals of different ages that were killed by rapid burial.

Small and hence juvenile valves are usually subelliptical in shape and reach a ratio of height to length of more than 0.8 (0.83 in PIW 1997IV30a), whereas large individuals usually have a ratio of height to length of 0.66 to 0.68. Accordingly, the posterodorsal auricle is much longer in those specimens and the auricle angle includes occasionally more than 135°.

In accordance with the increase in size, small individuals have a dentition consisting of two teeth, whereas large specimens have three or, rarely, four teeth.
Most of the examined specimens are preserved bivalved. As they were dissolved from shell hash layers with disarticulated or even fragmented sclerites of trilobites, hyoliths, chancellorids, echinoderms and other fossil groups, this suggests that the individuals lived infaunally and were normally preserved in their original habitat.

Size and growth
Lengths of the internal molds range from 680 to 2,250 μm, heights from 460 to 1750 μm, and width of the internal molds from 240 to about 850 μm. The values are roughly normally distributed, but the number of the measured specimens (N=22) is too small to permit statistically significant analyses.

The average ratio of anterior length to total length increases with growing overall length of the valves. This indicates that the apex moves to a progressively central position during life-time.

Regression curves of width to length and height to length (Fig. 6) indicate that allometric growth is insignificant for the major axes.

Shell structure
One specimen of the examined material is preserved with a partly limonitized shell that allows reconstruction of details of the shell. This specimen shows an external surface with faint concentric growth lines which were reinforced during diagenesis and weathering processes and fine radial striae which we interpret as to depict the radial arrangement of primarily aragonitic fibres. Corroded areas on the valves permit the view of the middle and inner shell layers that now consist of crystallite bundles arranged obliquely to the horizontal and radial axes of the shell (Fig. 4B, F). They permit identification of an irregular prismatic layer. This structure of the inner shell layer is similar to, although not identical with, the aragonitic, columnar prismatic shell structure described from P. runnegari by Runnegar and Bentley (1983). Polygons on the inner surface as noted from P. runnegari (Runnegar and Bentley, 1983: fig. 4) were not observed in P. sarhroensis.

Comparison
The differences between the species of Pojetaia are remarkably small, but careful investigation of the material indicates that these minor differences are sufficient to characterize distinct species. The paucity of characters and the occurrence in different faunal provinces as well as a general parallelism in mollusc morphotypes between western and eastern Gondwana around the Lower-Middle Cambrian transition corroborate this concept of discrete species.

P. sarhroensis n. sp. equals P. runnegari Jell, 1980, in most respects. Differences exist in a smaller and less well defined posterior auricle, in the apparently larger posterior hinge tooth, and in the barely projecting umbones of internal molds in P. sarhroensis. The posterodorsal tip of the auricle in P. runnegari includes an angle of 110-120°.

P. ovata Chen and Wang, 1985 differs from P. sarhroensis in having a clearly larger, well defined posterior auricle, very similar to that in P. runnegari. The posterodorsal tip of this auricle includes an angle of 110-120°. However, unlike P. runnegari it has two to three hinge-teeth and corresponding sockets and a less clearly projecting umbo in internal molds, like P. sarhroensis.

P. elliptica Li and Zhou, 1986 (synonym: Jelliia elliptica Li and Zhou, 1986) has a similarly faintly developed auricle (and, thus, a similarly large auricle angle of up to about 135°), but differs in the more subelliptical shape of the valves.

As mentioned above, Fordilla germanica Elicki, 1994 from the Early Cambrian of eastern Germany has an elongate rather than oval lateral outline, subcentral umbones, and a small posterodorsal auricle and is hence tentatively placed under the genus Pojetaia. Pojetaia

Plate 1
Pojetaia sarhroensis n. sp. All from Jbel Arbouri section, sample horizon JAR-0,56.

1-3 Paratype, PIW 1996X32.1, silicified left valve. • 1. Internal view. (x40.) • 2. Detail, oblique dorsal view showing dentition consisting of three teeth that decrease in size anteriorly. (x75.) • 3. Oblique anterior view of hinge region with dentition and imperfectly preserved posterior ligament area. (x80.)

4 Paratype, PIW 1997IV1. Dorsal view of internal mold showing pattern of hinge teeth. (x50.)

5 Paratype, PIW 1997IV1. Right lateral view of partly exfoliated specimen, showing muscle tracks along pallial line. (x50.)

6 Paratype, PIW 1997IV2. Right lateral view of largely exfoliated specimen, showing pallial line and imperfectly preserved anterior adductor muscle scar. (x50.)

7 Paratype, PIW 1997IV4. Lateral view of internal mold of hinge region showing peg-like infillings of sockets. (x75.)

8 Paratype, PIW 1997IV29. Lateral view of internal mold of imperfectly preserved small individual with rests of pallial muscle tracks. (x60.)

9 Paratype, PIW 1997IV3. Right lateral view of partly coated internal mold with series of pallial muscle tracks. (x75.)

10 Paratype, PIW 1997IV24. Dorsal view of internal mold, showing filled opisthodetic ligament slot and pattern of hinge teeth. (x75.) Arrow points to hinge tooth corresponding to transposed dentition in Fig. 12.

11 Paratype, PIW 1997IV26. Dorsal view of partly coated internal mold, showing pattern of hinge teeth. (x75.)

12 Holotype, PIW 1997IV25. Dorsal view of partly coated internal mold, showing pattern of hinge teeth and filled ligament slot. (x75.) Note transposition of hinge teeth in comparison to PIW 1997IV24 in Fig. 10.
germanica differs from the other species of the genus in the rather conspicuous elongation of the valves and the umbones that are short distance anterior to the center of the dorsal margin. It should be noted that the size of the holotype (Elicki, 1994: fig. 4,13) is indicated as being 3.0 mm, which would be the largest ever published specimen of an Early Cambrian peneiopod.

Elicki (1994) also figures a (normal sized) specimen identified as Pojetaia runnegari. The specimen is not described in the text, but comes from the same locality and stratum as P. germanica. It shows a remarkable similarity with the Australian material and has the relatively strongly projecting umbones, but its auricle is apparently less well defined and not completely preserved in the figured specimen. Additional material needs to be examined to evaluate the precise identity.

Pojetaia ostseensis Hinz-Schallreuter, 1995 was described from the Middle Cambrian (Triagnostus gibbus Zone) Essulans Limestone of Bornholm. Although the material is relatively large (length of the valves about 1.3 to 1.7 mm), the dentition with three distinct teeth and the comparatively elongate shape (length-to-width ratio 1.50 to 1.54) is relatively characteristic. The auricle angle is large (around 135°).

Table 1 gives an overview of the most important characters seen in the species of Pojetaia.
Figure 8. *Arhouriella opheodontoides* n. gen., n. sp. Reconstruction of hinge area. Scale bar equals 100 µm. Abbreviations: af=anterior fossette, hp=hinge plate, pl=posterior ligament area, u=umbro.

**SUBCLASS AND ORDER UNDETERMINATE**

**Family** Arhouriellidae n. fam.

**Diagnosis:** Shell equivalved, equilateral. Valves veneriform and suboval to subelliptical. Umbones prosogyrate. Dorsal margins of valves strengthened. Ligament amphidetic. Right valve with dentition consisting of two teeth that overhang the hinge plate.

*Arhouriella* n. gen.

**Type species:** *Arhouriella opheodontoides* n. gen., n. sp.

**Diagnosis:** Diagnosis of the family.

**Derivatio nominis:** Named after Jbel Arhouri.

**Discussion:** See discussion under *Arhouriella opheodontoides*.

*Arhouriella opheodontoides* n. gen., n. sp.  
Figs. 7, 8

**Holotype:** PIW 1997IV20, incomplete right valve (Fig. 7A-E).

**Paratype:** PIW 1997IV8, right valve.

**Locus typicus:** Jbel Arhouri section, east-central Anti-Atlas.

**Stratum typicum:** Sample horizon JAR-0.56, Jbel Wawrmast Formation, Brèche à Miacacea Member; Cephalopyge notabilis Zone, early Middle Cambrian.

**Derivatio nominis:** From the classical Greek ὄβετος, ἐσω (snake), and ᾦδαμ, ὑτόσσα (tooth); an allusion to the hinge-teeth that project like in the mouth of a snake.

**Diagnosis:** Diagnosis of the genus (because of monotypy).

**Description**  
The description is based on two right valves, one of which is incomplete, the other only bears a poorly preserved hinge area. The identification as right and left valves is based on (1) the oval shape of the valves with a better rounded posterior margin as in comparable Early Paleozoic forms, and (2) the presence of a faint imprint interpreted as posterior adductor muscle scar.

Shell apparently equivalved and roughly equilateral. Valves suboval to subelliptical, without distinct auricle. Umbo apparently slightly prosogyrate, projects faintly beyond the hinge. Exterior of valves with faint growth lines.

Interior of valves smooth, except for single, large adductor muscle scar in posterior position (Fig. 7H). Faint pallial commences at adductor muscle scar.

Best evidence for the morphology of the hinge and the ligament comes from the partially preserved, silicified right valve. The fragment includes the posterodorsal portion of the valve with the hinge and part of the ligament area so that the most important characters are visible.

Internally is a well developed hinge plate the surface of which is covered with fine growth lines. Apparently, this hinge plate was partly covered with the ligament. The hinge plate is slightly concave in ventral view and forms a platform that undercuts the dentition and is defined posteriorly by a narrow platform which is interpreted as a ligament area. In its anterior part, the hinge plate is strongly convex in transverse section and slopes rapidly towards the valve floor so that it consists of a narrow ridge bordered dorsally by a groove (Fig. 7B, E). In contrast, its sector beneath the hinge teeth is wider and nearly plain.

Two sites of apparent ligament attachment are recognizable. One is a fossette anterior to the umbo that represents a ligament groove which continues posteriorly and ends close to the anterior of the hinge teeth. Another ligament area is located posterior and dorsal to the posterior hinge tooth and has a broad lancet shape (Fig. 7C). Slightly anterior to the beak the ligament was partly covered dorsally by a transversely narrow band of the dorsal valve margin (Fig. 7B, D), whereas no dorsal cover is present at the ligament area posterior to the beak.

The dentition consists of two teeth, which originate close to the dorsal margin of the valve, although a hinge plate is developed. These teeth project ventrally and are somewhat undercut (Fig. 7E). The anterior tooth originates with a comparatively massive base directly at the dorsal margin, whereas the posterior tooth is in a slightly more ventral position because of the dorsally adjacent ligament area.

**Discussion**  
This arrangement of teeth and ligament area is totally new and unexpected for Cambrian pelecypods. It suggests the presence of an amphidetic and partly internal ligament that obviously was placed directly between the valve margins and could extend dorsally only at its anterior and posteriormost parts. Even beyond, the structure of the hinge plate that undercuts the teeth suggests that at least the anterodorsal part beneath the anterior tooth, but probably the entire middle sector of the hinge plate, was covered by ligament in an earlier ontogenetic stage. Thus, it may be concluded that the valves of *Arhouriella* were attached mainly by a long ligament in juveniles. The hinge teeth apparently
developed in a later stage and then projected over the now infunctonal middle part of the hinge plate. This serves for the remarkable absence of clearly developed sockets.

This condition strongly differs from the strictly opisthocelic ligament in Fordilla and Pojetaia. The dentition in Arhouriella also suggests an advanced rather than a primitive state. These conditions are unlike the primordial taxodont condition as in Fordilla and Pojetaia.

THE ORIGIN OF THE PELECYPods

The few findings of Early and Middle Cambrian pelecypods and their mostly imperfect preservation and limited amount of characters do not permit a well-based reconstruction of their early phylogeny and origin. Most of the recognizable characters seen in Pojetaia and Fordilla are more-or-less directly related to the small sizes of these animals, such as the few hinge teeth, the straight ligament, and the dispersed pallial muscle insertions (Runnegar and Bentley, 1983). It is remarkable, however, that pelecypods remain relatively poorly diverse in the second burst of the Cambrian explosion, when a great number of different fossil groups attained large numbers of species and individuals.

Two facts should be emphasized that shed some light on the aspects of pelecypod phylogeny and origin. Reconstructions of the earliest pelecypods with originally exogastronic coiling (Peel, 1991a) appear sound. This would suggest that pelecypods did not develop from helcionelloid via rostroconch ancestors as commonly assumed (Runnegar and Pojeta, 1974; Pojeta, 1980; Runnegar and Bentley, 1983), because rostroconchs are now widely accepted as endogastric and derived from the endogastric Helcionelloidea (Peel, 1991a, b; Geyer, 1994). This, in turn, does not support arguments for a possible epifaunal origin of pelecypods although a reconstruction of earliest pelecypods as epifaunal suspension feeders (Tevesz and McCall, 1976) may be hypothesized. However, it remains a puzzling fact that the apparent multiple paired pedal muscle scars seen in Fordilla and Pojetaia leave little space to accommodate a gill apparatus of appropriate size for suspension feeding although Runnegar and Bentley (1983) argued that Pojetaia and Fordilla are small enough to operate as suspension feeders without specialized organs like juvenile specimens of the extant Nucula. Although the specimens examined during this study come from shell hash layers, most of them are preserved bivalved. This indicates that they lived infaunal and that the sampled horizon represents their original habitat.

Early pelecypods apparently do not show a constant pattern of distinct muscle scars. The number and size of muscle scars seen in Pojetaia sarhoensis vacillates. This suggests that the muscle attachment is derived from a thin band of attached tissue concentric to the apex. Such a band is split into a rough track of muscle imprints rather than it depicts discrete pattern of scars. It is hence doubtful whether all the muscle scars can be directly compared among species or even genera although groups representing subsequent anterior pedal retractor muscle scars or anterior adductor muscle scars can be identified (compare Pojeta and Runnegar, 1985).

Fordilla and Pojetaia both share an opisthocelic ligament and simple dentition, which is interpreted as the primordial condition in the pelecypods that gave rise to the later nuculides and mytilooides (Jell, 1980; Runnegar and Bentley, 1983; Pojeta and Runnegar, 1985). In this light, the arrangement of well developed teeth and an amphidetic and partly internal ligament in Arhouriella n. gen. is totally unexpected. This form cannot be accommodated under the Nuculoida and even suggests the presence of a second subclass of pelecypods in the early Middle Cambrian. However, the morphological details visible on the studied material are insufficient to permit further conclusions. In addition, it seems inappropriate in the present state of knowledge on Cambrian pelecypods to base hypotheses on systematic affinities and early phylogeny on the Cambrian pelecypod record.

ACKNOWLEDGEMENTS

The authors are indebted to Sha Jingeng, who made available some of the Chinese literature and translated parts of the Chinese descriptions. Thanks are also due to Shu Degan for Chinese literature. Wolfram Heldmaier kindly provided information on the Jbel Arhouri section and thin sections of the sample horizon. In addition, this study benefitted from discussions with F. T. Fürsich and Sha Jingeng on Arhouriella and from a helpful review by P. Jell (Brisbane). The SEM micrographs were taken in the Biozentrum of the Würzburg University (ZEISS DSM 962) and in the Fachbereich für Geowissenschaften, Universität Bremen (CamScan 44).

REFERENCES


Geyer, G. 1989. Late Precambrian to early Middle Cambrian lithostratigraphy of southern Morocco. *Beringeria,* 1, 115-143.


Yermak, V. V. 1986. Rannekembrijskie fordillidy (Bivalvia) severa Sibirskoj platformy. [Early Cambrian fordillids (Bivalvia) from the northern Siberian Platform.] In: Biostratigrafiia i paleontologija kembrija Severnoj Azii. [Biostratigraphy and palaeontology of the Cambrian of northern Asia.] (Ed. I. T. Zhuravleva). Trudy Instituta geologii i geofiziki, Sibirskoe otdelenie, Akademija nauk SSSR, 669, 183-188. [In Russian.]


Manuscrito recibido: 31 de julio, 1997
Manuscrito aceptado: 23 de junio, 1998