SIPHOPFENDERINA GEN. NOV. (TYPE-SPECIES ARENOBULIMINA GEYIKENSIS SOLAK, 2022), A PRIMITIVE PFENDERINID FORAMINIFERA FROM THE CRETACEOUS OF NEOTETHYS

Felix Schlagintweit1 & Michel Septfontaine2

INTRODUCTION

Pseudokeriotheca represents “a texture of external chamber walls in Mesozoic and later agglutinated foraminifers consisting of uniform, parallel, radial elements covered by some kind of tectum” (Hottinger, 2006, p. 29). With respect to higher taxonomic rank, pseudo-keriotheca have been recorded from the orders Loftusiana Kaminski, Textulariida Delage & Hérouard, and Nezzazatina (Schlagintweit and Yazdi-Moghadam, 2022, for further details). Pseudokeriotheca is usually associated with a comparably thick, microgranular wall exhibiting delicate pores having diameters of usually 4 to 10 µm (e.g., Septfontaine, 1981). If present, this feature is of generic importance and should always be included in the diagnoses of the relevant taxa (see examples below). It is worth mentioning that no genus is defined on this feature alone, but always in combination with other characteristics such as test morphology (e.g., chamber arrangement, coiling type), internal test structures etc. The species Urgonina (Parurgonina) forojuliensis Cuvillier et al., 1968 for example was originally described as a subgenus of the orbitolinid Urgonina Foury & Moullade, 1966 from the Upper Jurassic of Italy. The presence of a pseudokeriotheca in Urgonina (Parurgonina) forojuliensis (not mentioned in the original description) indicates that it belongs neither to the Orbitolinidae nor to the genus Urgonina (Schoeder et al., 1975). In recent classifications of the agglutinated foraminifera, the genus Parurgonina Cuvillier et al., 1968 is included in the Parurgoninidae Septfontaine, 1988 (Kaminski, 2014). Other examples of foraminifera with pseudokeriothecal wall structure include the Middle Jurassic Conicopfenderina Septfontaine in Kaminski, 2000, the Lower Cretaceous Melathrokerion Brönnimann & Conrad, 1967, the Upper Cretaceous–Paleogene Chrysalityidae Orbigny, 1839 (e.g., De Castro, 1991), Paleogene Coskinolina Stache, 1875, Coleicos Hottinger & Drobro, 1980, and Barattolites Vecchio & Hottinger, 2007, and others. It is worth noting that the presence of pseudokeriotheca within the wall seems to be incompatible with any exoskeletal microstructure (hypo-dermic network or radial partitions of larger foraminifera; Septfontaine, 1981, for details). It may be due to differential hosing of symbionts (e.g., according to size) in different genera (Septfontaine, 2020). For the families Bio-koviniae Gušić and the Charentiidae Loeblich & Tappan, the presence of pseudokeriotheca is interpreted as of suprageneric taxonomic importance (Loeblich & Tappan, 1985; Gušić, 1977). For this reason, the genus Coskinolina Stache, 1875 (thick wall with pseudokeriotheca), for example, has been removed from the Orbitolinidae Martin (Douglass, 1960) and included within the Coskinolinidae Moullade, 1965 (Loeblich & Tappan, 1987). Solak (2021, p. 149), in a recent study on some Aptian orbitolinids from the Central Taurides of Turkey, reported “the presence of a pseudo-keriothecal wall-structure in the Cribellopsis species...(that)...has not been reported previously”. Neither is it reported from the type-species C. neoelongata (Cherchi & Schroeder, 1978) nor any other species of Cribellopsis Arnaud-Vanneau (e.g., Arnaud-Vanneau, 1980; Schlagintweit & Bucur, 2021), this form cannot, in our opinion, belong to this genus unless a pseudokeriothecal wall has been evidenced in the type-species. This would in consequence lead to the emenda-

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tion of the genus and the removal of Cribellopsis from the Orbitolinidae. Recently, a new benthic foraminifer species has been described as Arenobulimina geyikensis from the Aptian of the Central Taurides of Turkey (Solak, 2022). This species is differentiated from “all species hereto attributed to the genus Arenobulimina in the Lower Cretaceous by a larger test with a thick, pseudokeriotohekal wall” (op. cit., p. 42). It is worth mentioning, that the genus Arenobulimina Cushman, 1927 is included in the suborder Ataxophragmiina Fursenko, 1958 displaying a “wall... (roughly, coarsely) ...agglutinated typically with calcareous cement” (= non-canaliculate) (Kaminski, 2014, p. 102). Moreover, the genus Arenobulimina is recorded mostly from shales, as an inhabitant of open marine, deep water environments, contrary to the new taxon described herein (e.g., Reuss, 1845; Cushman, 1927; Gawor-Biedowa, 1969; Barnard & Banner, 1980; Frieg & Price, 1982; Hart et al., 1989; Besen et al., 2021).

Hence, in accordance with the taxonomic relevance of a pseudokeriotoheca as discussed previously, a new genus is introduced herein as Siphopfenderina gen. nov. with the new combination Siphopfenderina geyikensis (Solak, 2022). The taxonomic revision consequently includes a new suprageneric status of the taxon i.e., removed from the Ataxophragmiidae Schwager, 1877 and referred to the Pfenderinidae Smout & Sugden, 1962 herein.

MATERIAL AND METHODS

The present study is based on re-illustrations of some type-specimens from the Aptian of Turkey (Solak, 2022; with kind permission from the Micropaleontology journal editor). Other Lower Cretaceous material illustrated herein comes from the Aptian of Cantabria (northern Spain), and central Iran. Upper Cretaceous material refers to specimens from the Cenomanian Sarvak Formation of SW Iran, re-illustrated specimens from Radoičić (1980) coming from Coniacian-Santonian? strata of western Serbia, and the lower-middle Campanian of Brač Island, Croatia (Tab. 1). The depository of the material is as follows:

- The Turkish type-material is stored in the collection of Palaeontology at the General Geology Laboratory, Department of Geological Engineering (Mersin University, Turkey), as stated in Solak (2022).
- The material from northern Spain belongs to the Ramírez del Pozo Collection, that is stored at the Instituto Geológico y Minero de España, Tres Cantos (Madrid), Spain.
- The material from Central Iran belongs to the K. Rashidi collection, stored at the Department of Geology, University of Yazd.

SYSTEMATIC PALAEONTOLOGY

Class FORAMINIFERA d’Orbigny, 1826

Order LOFTUSIIDA Kaminski and Mikhalevich in Kaminski, 2004
Suborder Orbitolinina Kaminski, 2004
Superfamily PFENDERINOIDEA Smout & Sugden, 1962
Family PFENDERINIDAE Smout & Sugden, 1962

Remarks: The family Pfenderinidae includes variously shaped, trochosparially coiled forms that may have pseudokeriotoheca (Septfontaine, 1988, p. 245, for detailed diagnosis).

Subfamily PSEUDOPFENDERINAE Septfontaine, 1988

Diagnosis: Test trochosparially coiled throughout. Siphonal canal situated axially, or massive axial columella made by interseptal pillars and calcite infilled material between pillars in advanced forms. No subcameral tunnel. Vertical radial partitions may be present in the last chambers of advanced genera. Aperture single associated with siphonal structure, or multiple associated with pillars (Septfontaine, 1988, p. 245).

Remarks: Septfontaine (1988) erected the subfamily Pseudopfenderininae including the two genera, Siphovalvula Septfontaine, 1988 (with axial siphonal canal = hollow columella in Septfontaine, 2020, p. 149) and Pseudopfenderina Hottinger, 1967 (with axial solid columella). Concerning the terminology used, Hottinger (2006, p. 11) defined a columella “as a solid trochospiral structure formed by the basal walls of spiral chambers coalescing around the coiling axis, as in many gastropod shells”. Gale et al. (2018, p. 269) removed Siphovalvula from the Pseudopfenderininae, instead including it in the new family Siphovalvulinae defined (besides other features) as “triserial, may later become biserial... (and with)... ‘paraporous wall’”. Leaving apart the problem of the distinction between pseudokeriotoheca or paraporous walls, Siphopfenderina gen. nov. with a trochospiere exhibiting numerous chambers per whorl cannot be included in the Siphovalvulinae. It is herein included within the Pseudopfenderininae due to its primitive pfenderinid morphology and multiserial coiling (see also Septfontaine, 2020).

Siphopfenderina gen. nov.

Type species Arenobulimina geyikensis Solak, 2022

Holotype: The holotype specimen is the subaxial section illustrated by Solak (2022) in plate 1, figure A, thin-section labeled Gc47H and deposited in the collection of Palaeontology at the General Geology Laboratory, Department of Geological Engineering (Mersin University, Turkey).

Etymology: The generic name is derived from the central siphon, combined with the name Pfenderina.

Diagnosis: Test free, elongate-conical, consisting of trochosparially coiled chambers arranged in a few sometimes irregularly whorls with a central siphon or hollow columella. The siphon may become larger in adult
Siphopfenderina gen. nov. (type-species Arenobulimina geyikensis Solak, 2022)

Table 1

<table>
<thead>
<tr>
<th>taxon</th>
<th>age</th>
<th>reference</th>
<th>formation, locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siphopfenderina geyikensis</td>
<td>Aptian</td>
<td>Solak, 2022</td>
<td>Polat Limestone, Anamas-Akseki platform, Central Taurides, southern Turkey</td>
</tr>
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<td>(Solak)</td>
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<tr>
<td>Siphopfenderina sp. aff.</td>
<td>late early Aptian</td>
<td>Schlagintweit &amp; Rashidi, 2022</td>
<td>Taft Formation, central Iran</td>
</tr>
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<td>geyikensis</td>
<td></td>
<td></td>
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<tr>
<td>Siphopfenderina sp. aff.</td>
<td>middle-late</td>
<td>Radoičić, 1980</td>
<td>Sarvak Formation, southwestern Iran</td>
</tr>
<tr>
<td>geyikensis</td>
<td>Cenomanian</td>
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<td>Santonian</td>
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<tr>
<td>Siphopfenderina ssp.</td>
<td>early-middle</td>
<td></td>
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<td></td>
<td>Campanian</td>
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chambers forming a deep open umbilicus. Proloculus spherical, in apical position. Wall thick imperforate microgranular with pseudokeriotheca and covered by a tectum; septal walls solid.

Comparisons: Pseudopfenderina Hottinger, 1967 differs from Siphopfenderina above all by its solid columella and the lack of a pseudokeriothecal wall (Fig. 1.1-1.5). Siphovalvulina Septfontaine, 1988posses a central siphon like Siphopfenderina, but differs from the latter by a triserial test that may later become biserial (see Gale et al., 2018). It is worth mentioning that the central siphon or hollow columella (= pseudoumbilicus in Solak, 2022) is poorly visible in the illustrated specimens from Turkey. Many of them are subaxial, tangential or oblique sections, where the central siphon is not sectioned at all or only partly, randomly. Following the interpretation of Gale et al. (2018), the siphon is formed by addition of the interior wall of the successive chambers. Last but not least, Siphopfenderina gen. nov. may also be compared with the Maastrichtian Pseudochablaisia Schlagintweit, Septfontaine & Rashidi, 2019 (Fig. 1.6-1.8). This low-trochospirally coiled taxon shares with Siphopfenderina gen. nov. the presence of a central siphon and pseudokeriotheca. In Pseudochablaisia however, “a septal button (defined by Septfontaine, 1977) occurs in the basal center of the chambers at the floor of the simple slit-like aperture appearing as a dome-shaped knob” (Schlagintweit et al., 2019, p. 111).

Other species: Besides Siphopfenderina geyikensis (Solak) comb. nov., the taxon described by Arnaud-Vanneau (1980) as Arenobulimina cochleata from the upper Barremian-lower Aptian of southern France is assigned to the genus Siphopfenderina. The central axial siphon (= columelle centrale in Arnaud-Vanneau, 1980, p. 449) is well discernible in the axial sections shown in pl. 81, figs. 11-13. Arenobulimina corniculum Arnaud-Vanneau, 1980 might also belong to Siphopfenderina showing a twisted axial siphon and, according to Solak (2022, p. 404), a pseudokeriothecal wall (Arnaud-Vanneau, 1980, pl. 81, fig. 2). Also, for Arenobulimina corniculum, Arnaud-Vanneau (1980, p. 444) mentioned the presence of a “sorte de columelle” separating the chambers. Other specimens are clearly microgranular (pseudokeriotheca not visible) without agglutinated material compared to the deeper water “true” Arenobulimina. Thus, it gives evidence that the microgranular wall is (phylo)genetically separated from its isomorphic equivalent in deeper waters. It is worth noting that the general identification of the pseudokeriotheca depends on the quality of the thin section (e.g., thickness) and its state of preservation is often masked by diagenetic alteration (Vicedo et al., 2014; Solak, 2021). It is worth mentioning that pfenderinids (including Siphopfenderina) do not possess a so-called valvular tooth plate or dental plate (plaque dentaire in Arnaud-Vanneau, 1980, p. 444), instead there is a porous last chamber or sieve plate (Remond, 1964; Septfontaine, 1978). Species of Siphopfenderina might classically be differentiated by size and/or general morphology (Solak, 2022, tab. 1). This in turn means that species are defined in some cases by subjective features (more ..., less ...), and partly also with overlapping biometric ranges.

Siphopfenderina geyikensis (Solak, 2022) comb. nov. Fig. 2.1-2.6

1979 ? Valvulamina sp. – Cherchi, p. 365, pl. 24, figs. 1-4 (late Aptian-?Albian of Sardinia, Italy).
1980 Arenobulimina aff. corniculum Arnaud-Vanneau – Arnaud-Vanneau, p.445, pl. 82, figs. 1-4, 6-7 (fide Solak, 2022).
? 2012 Dobrogelina sp., Arenobulimina sp. – Marian & Bucur, figs. 5F, 5N.
2020 Nezzazatinella picardi – Solak et al., Fig. 11L.
*2022 Arenobulimina geyikensis n. sp. – Solak, p. 402, pls. 1-3.
Remarks The detailed description of Solak (2022) is fully adequate. The term pseudoumbilicus used by Solak (2022) is herein replaced by central siphon or open (hollow) columella. Beside the occurrences in the Central Taurides, Turkey and southeastern France, we suggest that Siphopfenderina geyikensis is also present in the upper Aptian of Sardinia, Italy (Cherchi, 1979: ? Valvulammina sp.), and perhaps also in the Aptian of northern Spain and central Iran (see the following remarks on Siphopfenderina sp. aff. geyikensis).

Siphopfenderina sp. aff. geyikensis (Solak)

Fig. 2.7-2.21

Remarks The specimens from the Aptian of northern Spain (Figs. 2.8-2.9, 2.11, 2.14) and central Iran (Figs. 2.7, 2.10, 2.12-2.13, 2.15-2.21) are here treated as a single morphotype exhibiting high variability, and showing similarities to some smaller specimens of Solak (2022, pl. 1, fig. H) re-illustrated herein in Fig. 2.6. The Turkish type-material shows generally larger dimensions, but with overlapping size-ranges to the Spanish and Iranian material. The number of whorls is three to six; transverse sections show six chambers per whorl.

Dimensions: wall thickness up to 0.065 mm (Solak, 2022: 0.05 to 0.11 mm); test diameter up to 0.57 mm; test height up to 0.75 mm.

Siphopfenderina ssp.
Figs. 2.22-2.30

2017 Arenobulimina sp. – Solak, figs. 11F-G (late Cenomanian of Turkey), 12K-L, 13U2 (late Maastrichtian of Turkey).
2019 Nezzazatinella picardi – Solak et al., figs. 13F (late Cenomanian of Turkey).

Remarks: Siphopfenderina ssp. is morphologically variable, a common, high-conical morphotype is treated in open nomenclature herein. It has been referred to as
Siphopfenderina gen. nov. (type-species Arenobulimina geyikensis Solak, 2022)

Fig. 2 Siphopfenderina geyikensis (Solak, 2022) gen. et comb. nov. from the Aptian of Turkey (1-6; Solak, 2022: Pl. 1, fig. a, pl. 2, fig. 1, pl. 1, fig. e, pl. 2, fig. b, pl. 1, fig. c, pl. 1, fig. h). Siphopfenderina sp. aff. geyikensis (Solak) from the Aptian of central Iran (7, 10, 12-13, 15-21), and Cantabria, northern Spain (8-9, 11, 14). Siphopfenderina ssp. from the Coniacian-Santonian? of Serbia (22-26), Cenomanian of SW Iran (27-28), Campanian of Croatia (29-30). Abbreviations: co. = (hollow) central columella, fo. = foramen, p.k. = pseudo-keriotheca, pr. = proloculus, se. = septum.
Foraminifer F-66, *Arenobulimina* sp., and *Nezzazatlinella picardi* in upper Cenomanian to upper Maastrichtian shallow water carbonates of Croatia, Serbia, and Turkey (see synonymy). The central siphon is clearly visible in the specimens illustrated by Radoićić (1980) (Fig. 2.22, 2.24).

**DISCUSSION**

The presence of ‘primitive’ pfenderinid morphotypes such as *Siphopfenderina* in stratigraphical levels above morphologically more advanced forms like *Pfenderina neocomiensis* (Pfender, 1938) (late Berriasian-Valanginian) or *Pfenderina globosa* Foury, 1968 (Barremian) is intriguing. During Early and mid-Cretaceous times, the oceans suffered several anoxic events with effects on carbonate shallow water (micro)fauna (e.g., extinctions, blooming) with causalities still not fully understood such as the early Aptian anoxic event OAE1a (selli event) (e.g., Jenkyns, 2010; Strasser et al. 2001). In an epigenetic perspective, it may be that this peculiar, apparently retrograde, simpler morphology among pfenderinids is the result of some reverse evolution mechanism (*sensu* Guex, 2016 and discussed by Septfontaine, 2020) for larger lituloids related to extreme environmental conditions during warming of the oceans, locally or globally. Iterative evolution within the siphovalvulinids-pfenderinids clade during the Mesozoic (Septfontaine, 2020) could be related to repetitive periods of stress due to warming and anoxic events in an epigenetic perspective of evolution not affecting the genome.

This must of course be tested with other taxa in phylogenetic series through time against other OAE episodes. This morphological transformation seems possible within lituloid ‘plexus’ displaying a small size and rather simple interior contrary to other advanced very complex morphologies (*OrbitopSELLA, Anchispirocyclina* or alveolinids etc.) which are fixed in their complicated characters.

**CONCLUSIONS**

A new taxon is described as *Siphopfenderina* based on *Arenobulimina geydikensis* Solak, 2022 (Aptian of Turkey) from shallow carbonate environments with a microgranular wall and pseudokeriotheca belonging to the pfenderinids clade, subfamily Pseudofpenderinidae. *Siphopfenderina* displays a rather primitive morphology, with a central hollow columnella but without internal complicated microstructures compared with the more evolved ancestor *Pfenderina* in the Lower Cretaceous. The presence of an apparently primitive taxon above more evolved ascendants may be the result of stressful environmental conditions related to anoxic events in the Lower to middle Cretaceous, according to a mechanism of regressive evolution under stress (reverse evolution, *sensu* Guex, 2016) during episodes of warming. Further records from Spain, Italy, and Iran provide further data for the wide distribution of *Siphopfenderina* in Lower Cretaceous carbonate platforms. Furthermore, it may be suspected that many records of mid-Upper Cretaceous siphovalvulinids (bi-/triserial) (Liassic–Early Aptian) in the literature in fact belong to the multiserial *Siphopfenderina* (?Barremian–Campanian). The literature research also concludes that *Siphopfenderina* is also present in the Upper Cretaceous.

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