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

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Abstract The presence of a pseudokeriothecal wall structure is traditionally given a generic or even higher taxonomic status (in association with other features). A new trochospirally coiled taxon displaying a thick wall with pseudokeriotheca and a central siphon (hollow columella) is herein described as *Siphopfenderina* gen. nov. Such a taxonomic reappraisal is based on original figures and description of *Arenobulimina geyikensis* Solak. It is herein included within the Pseudopfenderininae due to its primitive "pfenderinid"-like morphology. *Siphopfenderina geyikensis* (Solak) comb. nov. was described from Aptian neritic Urgonian-type carbonates of the Taurides (Turkey) and said to be the only species of the genus *Arenobulimina* Cushman (family Ataxophragmiidae) especially due to such a type of wall structure. *Arenobulimina* is a typical (outer) shelf taxon, smaller in size, and with a thin and typically coarsely agglutinated wall. Other occurrences of *Siphopfenderina* gen. nov. are described in open nomenclature from the Aptian of Spain and Central Iran, as well as the Upper Cretaceous of Serbia, Croatia and Iran. *Arenobulimina cochleata* Arnaud-Vanneau from the Lower Cretaceous of France is assigned to *Siphopfenderina* herein. The taxonomic discrimination of these other species might be related to size and morphology criteria that requires further research.

Keywords: Foraminifera, taxonomy, wall structure, pseudokeriotheca, Lower Cretaceous

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-keriothecae have been recorded from the orders Loftusiina Kaminski, Textulariida Delage & Hérouard, and Nezzazatina (Schlagintweit and Yazdi-Moghadam, 2022, for further details). Pseudokeriotheca is usually associated with a comparably thick, micrgranular 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* (Schroeder 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 *Chrysalidina* Orbigny, 1839 (e.g., De Castro, 1991), Paleogene *Coskinolina* Stache, 1875, *Coleiconus* Hottinger & Drobne, 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 (hypodermic network or radial partitions of larger foraminifera; Septfontaine, 1981, for details). It may be due to differential housing of symbionts (e.g., according to size) in different genera (Septfontaine, 2020). For the families Biokovinidae 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, pseudokeriothekal 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 pseudokeriotheca 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 Paleontology 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 Insituto 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, trochospirally coiled forms that may have pseudokeriotheca (Septfontaine, 1988, p. 245, for detailed diagnosis).

Subfamily PSEUDOPFENDERININAE Septfontaine, 1988
Diagnosis: Test trochospirally coiled throughout. Siphonal canal situated axially, or massive axial columella made by interseptal pillars and calcitic 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 Pseudopfendererininae including the two genera, *Siphovalvulina* 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 *Siphovalvulina* from the Pseudopfenderininae, instead including it in the new family Siphovalvulinidae defined (besides other features) as “triserial, may later become biserial… (*and with*)…“paraporous wall”. Leaving apart the problem of the distinction between pseudokeriothecal or paraporous walls, *Siphopfenderina* gen. nov. with a trochospire exhibiting numerous chambers per whorl cannot be included in the Siphovalvulinidae. 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 Gç47H and deposited in the collection of Paleontology 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 trochospirally coiled chambers arranged in a few sometimes irregularly whorls with a central siphon or hollow columella. The siphon may become larger in adult

Table 1

taxon	age	reference	formation, locality
Siphopfenderina geydikensis (Solak)	Aptian	Solak, 2022	Polat Limestone, Anamas-Akseki platform, Central Taurides, southern Turkey
Siphopfenderina sp. aff. *geydikensis*	Aptian	Ramírez del Pozo, 1971	?, northern Spain
Siphopfenderina sp. aff. *geydikensis*	late early Aptian	Schlagintweit & Rashidi, 2022	Taft Formation, central Iran
Siphopfenderina ssp.	middle-late Cenomanian	-	Sarvak Formation, southwestern Iran
Siphopfenderina ssp.	?Coniacian, ?Santonian	Radoičić, 1980	Štira Limestone, Gučevo Region, western Serbia
Siphopfenderina ssp.	early-middle Campanian	Gušić & Jelaska, 1990 Cvetko Tešović et al., 2001	Gornji Humac and Pučišća formations, Brač Island, Croatia

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, 1988 posses 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 posses 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 (Redmond, 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 ? *Valvulammina* 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.

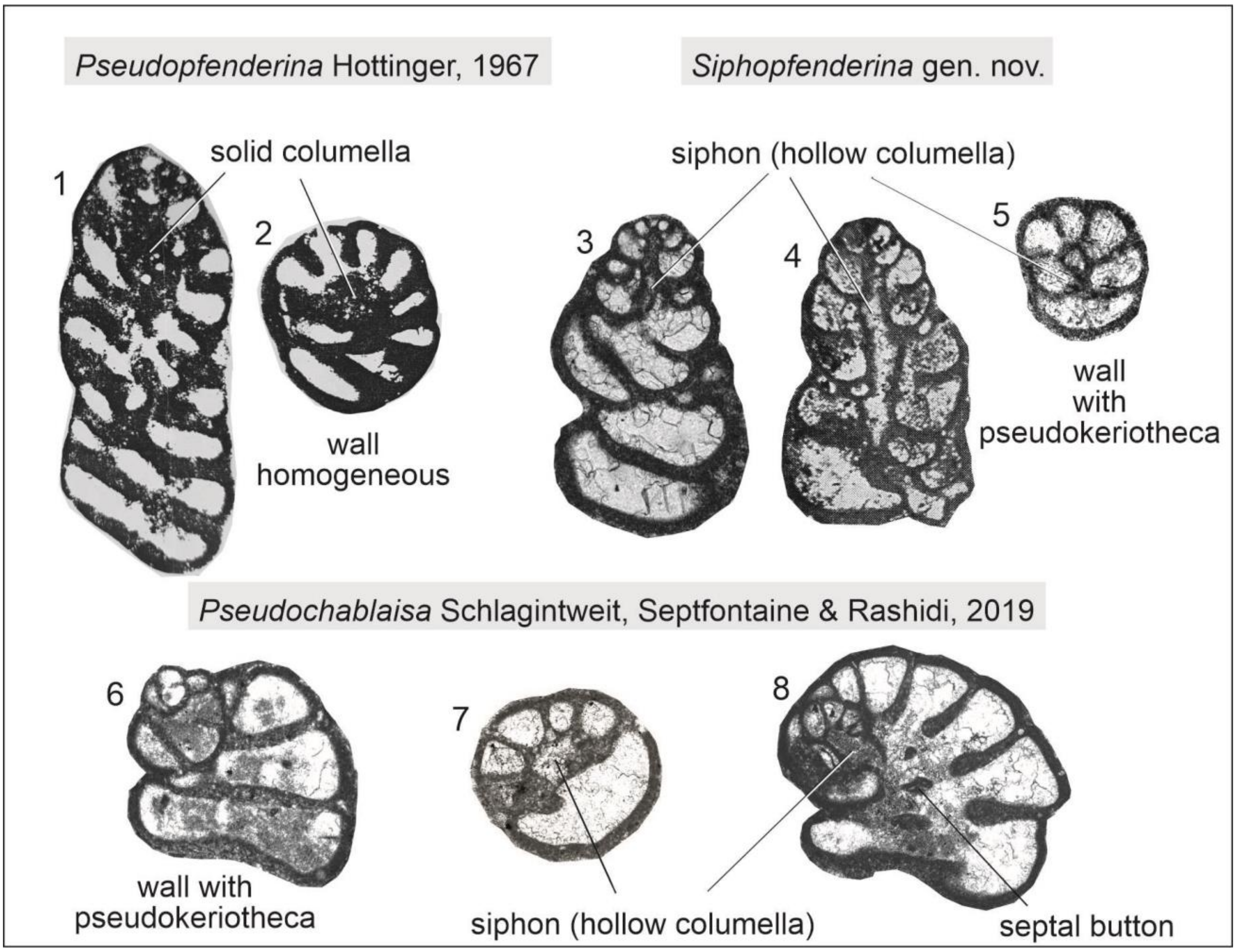

Fig. 1 Comparison between *Pseudopfenderina* Hottinger (1-2), *Siphopfenderina* gen. nov. (3-5) (without scale), and *Pseudochablaisia* Schlagintweit, Septfontaine & Rashidi, 2019 (6-8). 1-2: from Hottinger (1967, pl. 19, figs. 9 and 16, Liassic of Morocco. 3: Aptian of Spain (see fig.1.9); 4: from Radoičić (1980, pl. 5, fig. 1, Upper Cretaceous, ?Coniacian, ?Santonian of Serbia). 5: Aptian of Iran (see fig. 1.7). 6-8: from Schlagintweit et al. (2029, fig. 7A, 7B, 6F = holotype, Upper Maastrichtian of Iran).

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

1980 Foraminifer F-66 – Radoičić, pl. 5, figs. 1-7 (Coniacian? Santonian? of Serbia).
2017 *Arenobulimina* sp. – Solak, figs. 11F-G (late Campanian of Turkey), 12K-L, 13U2 (late Maastrichtian of Turkey).
2019 *Arenobulimina* sp. – Solak et al., fig. 11O-Q (late Maastrichtian of Turkey)
2020 *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

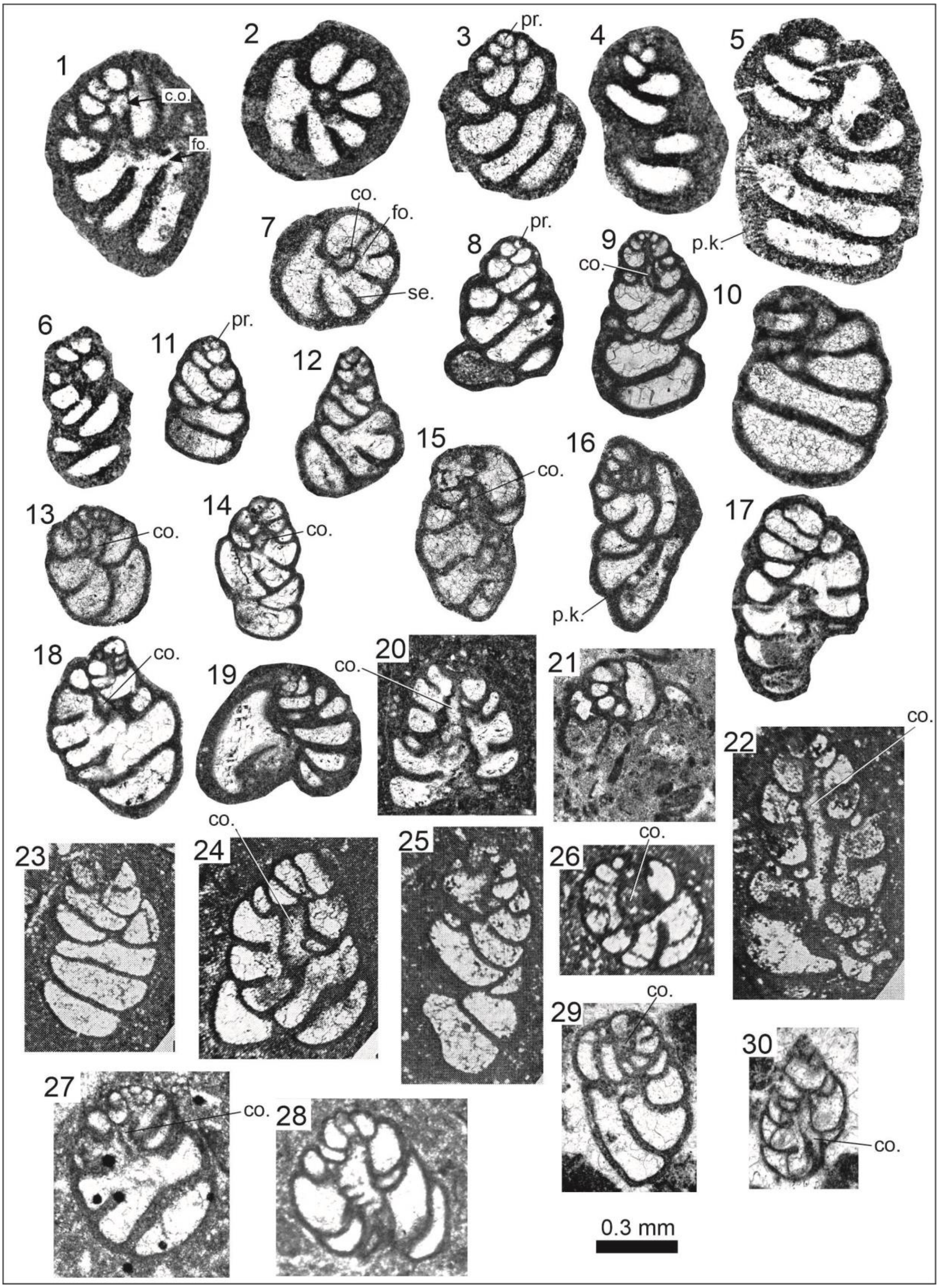

Fig. 2 *Siphopfenderina geyikensis* (Solak, 2022) gen. et comb. nov. from the Aptian of Turkey (1-6; Solak, 2022: Pl. 1, fig. a, pl. 2, fig. 1, pl. 1, fig. e, pl. 2, fig. b, pl. 1, fig. c, pl. 1, fig. h). *Siphopfenderina* sp. *aff. geyikensis* (Solak) from the Aptian of central Iran (7, 10, 12-13, 15-21), 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 *Nezzazatinella 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 Radoičić (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 lituolids) 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 lituolid ´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 Pseudopfenderinidae. *Siphopfenderina* displays a rather primitive morphology, with a central hollow columella 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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