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Siphonal zone structure in the cuttlebone of *Sepia officinalis*

Larisa A. Doguzhaeva[1] · **Elena Dunca[1]**

Abstract The evolutionary process through which the siphonal zone of the cuttlebone of *Sepia* replaced the tubular siphuncle seen in other shelled cephalopods is poorly understood. Recently, porous connecting stripes, interpreted as homologous to connecting rings of tubular siphuncles, were revealed in *Sepia* (*Acanthosepion*) cf. *savignyi* (Geobios, 45:13–17, 2012). New data on the siphonal zone structure are herein demonstrated through SEM testing of 16 beach-collected cuttlebones of *Sepia officinalis* from Vale do Lobo, southern Portugal. In examined cuttlebones, the organic connecting stripes are mineralized along their peripheries where they are attached to septa by inorganic–organic porous contacting ridges. The contacting ridges consist of globular crystalline units within an organic matrix; each globule is a stack of rounded alternating organic and mineralized microlaminas parallel to the septal surface; mineralized microlaminas contain carbonate microgranules. Porous connecting stripes together with the contacting ridges may serve as transport routes for the cameral liquid used in buoyancy regulation. The contacting ridges appear to reinforce contacts between the connecting stripes and septa, and may strengthen shell resistance to changing environments. Lamella–fibrillar nacre in septa is demonstrated in *Sepia* for the first time. Comparison of *Sepia* and *Spirula* reveals the common character of their phragmocones, the slit-like shape of the permeable zones between chambers and the siphuncle. Narrowing of the permeable zones may provide shell resistance to high hydrostatic pressure; however, the essentially dissimilar relative length of the permeable zones may results in different capabilities of two genera for buoyancy regulation. In *Sepia*, long narrow porous inorganic–organic permeable connecting stripes and contacting ridges may allow for rapid buoyancy regulation which would lead to environmental plasticity and higher species diversity.

Keywords *Sepia* · Cuttlebone · Siphonal zone · Connecting stripes · Contacting ridges · Lamella–fibrillar nacre

Introduction

Structure and ultrastructure of siphonal zone in *Sepia* are, with high probability, effective tools in rapid buoyancy regulation, in response to environmental variability, and high resistance of a cuttlebone against increased hydrostatic pressure. The siphonal zone structures may account for variation in habitats, broad geographic distribution and high species biodiversity of *Sepia*. Since Denton and Gilpin-Brown (1961) revealed that *Sepia* changes buoyancy by varying the amounts of liquid within the chambers of the cuttlebone and suggested that "liquid is probably moved in and out of the cuttlebone by an osmotic mechanism…", structure and ultrastructure of the siphonal zone in cuttlebones have received little attention (see Bandel and Boletzky 1979; Birchall and Thomas 1983; Ward and Boletzky 1984; Tanabe et al. 1985; Sherrard 2000; Gutowska et al. 2010). The only barrier in the way of the cameral liquid transport is thought to be "the yellowish coloured siphuncular membrane covering the siphuncular wall" (Denton and Gilpin-Brown 1961: pp. 341, 342). Recently, the segmented porous

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band-like shell structures covering the outside "openings" of chambers in siphonal zone, termed connecting stripes, were described in naturally cleaned beach-collected cuttlebones of *S. (Acanthosepion) cf. savignyi* Blainville, 1827 (Doguzhaeva and Mutvei 2012). The connecting stripes, like the connecting rings of ammonoids (Mutvei et al. 2004, 2010; Mutvei and Dunca 2007; Doguzhaeva et al. 2011), show segmented structure and fibrous porous ultrastructure and are considered to be homologous to the connecting rings in other cephalopods which have fully developed siphonal tubes (Doguzhaeva and Mutvei 2012; Doguzhaeva and Dunca 2014; herein).

We herein describe the structure and ultrastructure of the siphonal zone in cuttlebones of nekto–benthic common cuttlefish *Sepia officinalis* Linnaeus, 1758 that is abundant in eastern Atlantic and the Mediterranean Sea (Boletzky 1983). *S. officinalis* exhibits high physiological flexibility (Guerra 2006) possibly necessitated by changing environment during seasonal migrations between inshore (2–4 m) in summer and offshore (100–200 m) in winter (Sobrino et al. 2002; Guerra 2006). Presumed functional significance of the described structural elements of siphonal zone—connecting stripes and contacting ridges—is discussed. An attempt is undertaken to compare the siphonal zone structure of *Sepia* with siphonal tube structure in *Spirula*. Lamella–fibrillar nacre, herein revealed in septa of *S. officinalis*, is considered to be a negative factor in consideration of the hypothesized origin of cuttlebones from gladii by means of their secondary mineralization (Bonnaud et al. 2006).

Materials and methods

Studied material consists of 16 dry cuttlebones, naturally cleaned from soft tissues, of *S. officinalis* which were collected by ED along a beach in Vale do Lobo, southern Portugal in 2006–2007. Size range of available cuttlebones is 30–150 mm. Available cuttlebones were either fractured or cut transversally and longitudinally. The inside surfaces of the cuttlebones were analyzed using a Hitachi 4300 Scanning Electron Microscope. Specimens were either untreated or etched with glutaraldehyde/acetic acid/alcian blue solution. The solution contains 1:1 of glutaraldehyde and acetic acid with additive of alcian blue powder. Components were mixed for 20–30 min using an ultrasonic heating machine at 40 °C and then filtered. Specimens were etched for 10–25 min at 30–40 °C, washed and dried.

For the structural comparison between the siphonal zone of *Sepia* and tubular siphuncle of *Spirula*, we used the earlier scanning electron microscope images of *Spirula* obtained by SEM testing of beach-collected shells from Cuba and Australia (Doguzhaeva 2000; Doguzhaeva et al. 2011).

Terminology and abbreviations

Connecting stripes (*cs*) Structural element in the siphonal zone of cuttlebones; permeable band-like segments attached to neighbouring septal edges of achoanitic septa; may allow for liquid exchange between chambers of the phragmocone and the soft tissue of the siphon for buoyancy regulation;

Contacting ridges (*cr*) The ridge-like structural element in the siphonal zone of cuttlebones; located on contacts between connecting stripes and septa; allow for septum/connecting stripe fusion and liquid exchange between chambers of the phragmocone and soft tissue of the siphon for buoyancy regulation;

Lamella–fibrillar nacre (=nacre Type II in Mutvei 1970) Coleoid-related type of nacre characterized by micro-laminated ultrastructure; each lamella consists of parallel aragonite fibres or rods with different orientations in consecutive lamellas which result in criss-cross pattern observed in split overlapping laminas;

Lamella–globular ultrastructure (*new term*) Ultrastructure formed by globular crystalline units within an organic matrix; each globular crystalline unit is a stack of rounded parallel to septal surface alternating organic and mineralized microlaminas; each mineralized microlamina consists of carbonate granules imbedded in organic substance; herein applied to contacting ridges;

Pillar zone (*pi*) Permeable spherulitic-prismatic lining of the septal neck and slit-like openings between neighbouring septal necks in *Spirula*;

Siphonal zone (Bandel and Boletzky 1979) Ventral or inner side of cuttlebone; performs liquid exchange between chambers of the phragmocone and soft tissue of siphon and provides shell buoyancy regulation;

Siphonal structure Applied herein for shell structure, rather than soft tissue cord, or siphon;

Siphuncle Synonym of tubular siphuncle (see below);

Tubular siphuncle Tubular shell structure coating the soft siphonal cord; consists of alternative non-permeable septal necks and permeable connecting rings.

Observations on siphonal zone structure of *S. officinalis*

Connecting stripes

Naturally cleaned and dried siphonal zones of cuttlebones show partially removed shrunken and fractured segmented band-like connecting stripes covering the

outside slit-like "openings" of cameras in the cuttlebone (Figs. 1, 2, 3). They are attached to the neighbouring septa in such a way that their posterior and anterior edges are attached to the adoral and adapical septal surfaces, respectively (Fig. 2). Between septa, the connecting stripes loosely cover the pillars in chambers (Figs. 3, 4). Connecting stripes seem to be relatively thick (Fig. 2), but their thickness could not be measured in our preparations. Connecting stripes are mostly organic (Figs. 2, 3), but are loosely mineralized along their peripheries near septa (Figs. 3, 4). They have numerous micropores about 0.1–0.01 μm in diameter. Mineralized portions of the connecting stripes reveal microgranular ultrastructure and microporosity (Figs. 4, 5). Connecting stripes are attached to septa by contacting ridges (Figs. 1, 2, 3, 4).
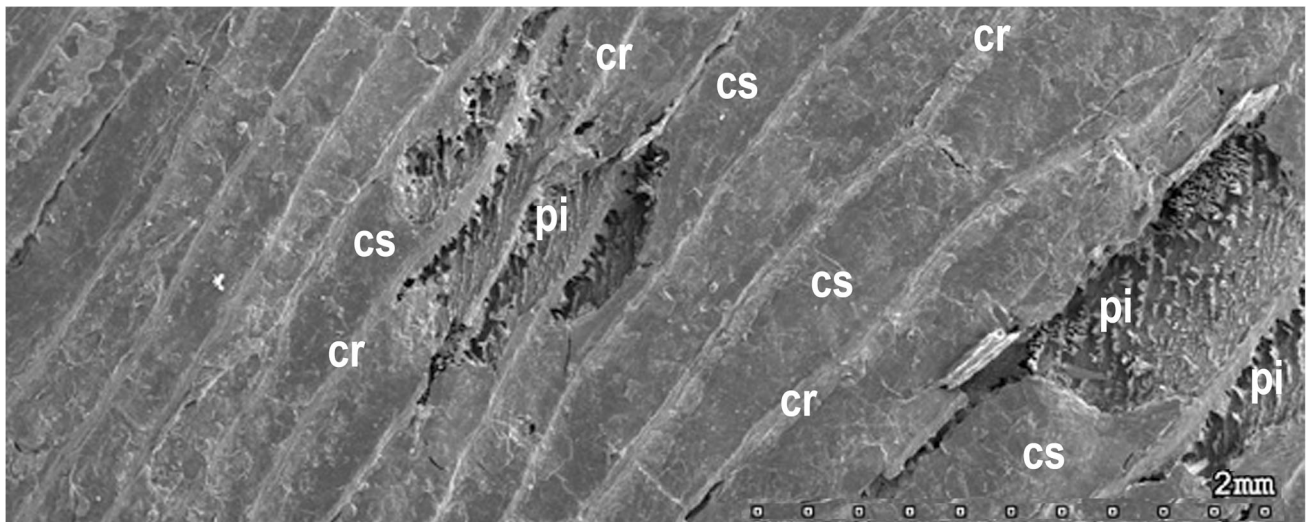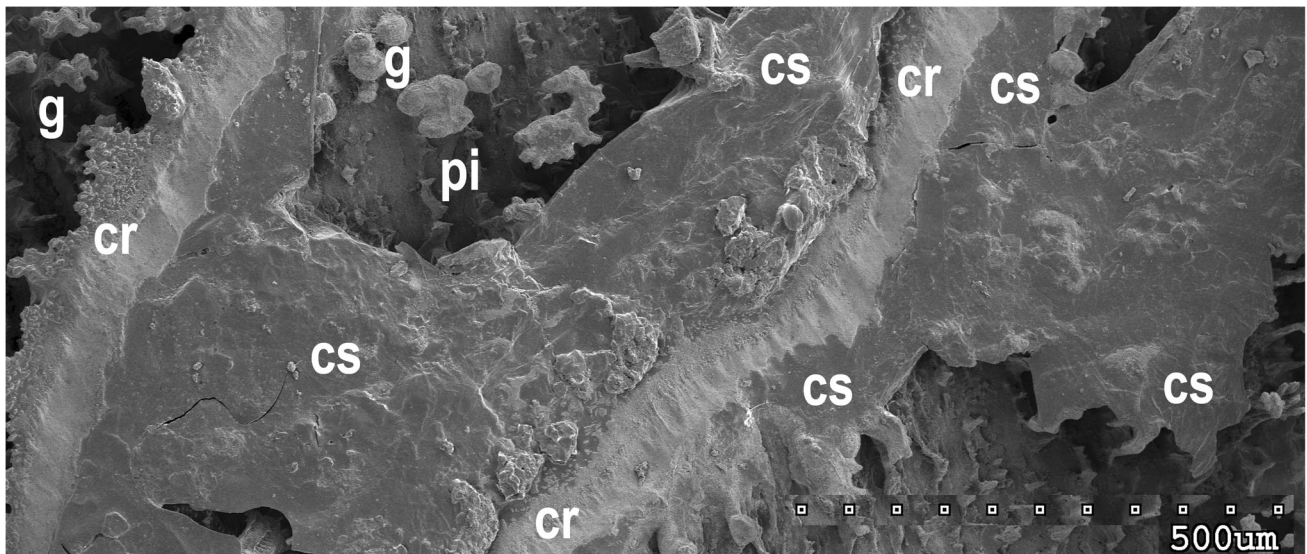

Fig. 1 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Ventral side of cuttlebone showing solid connecting stripes in periphery of siphonal zone and pillar structures in chambers seen where connecting stripes are broken. *Scale bar* is 2 mm. *cr* contacting ridge, *cs* connecting stripe, *pi* pillar structure
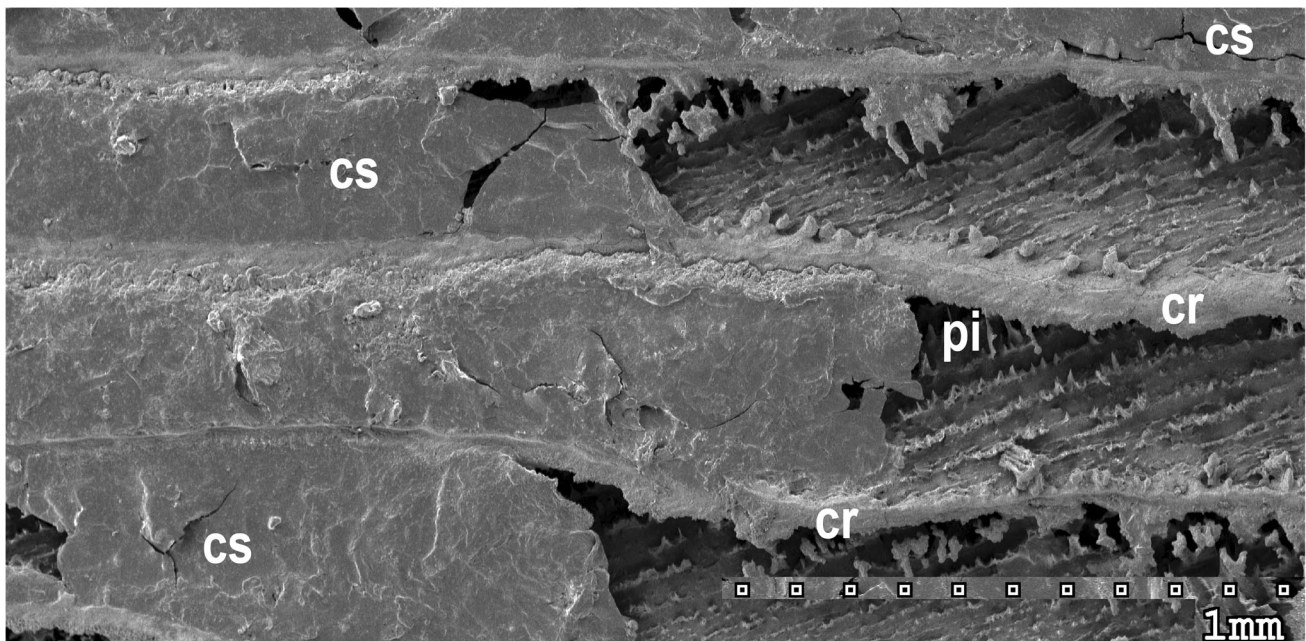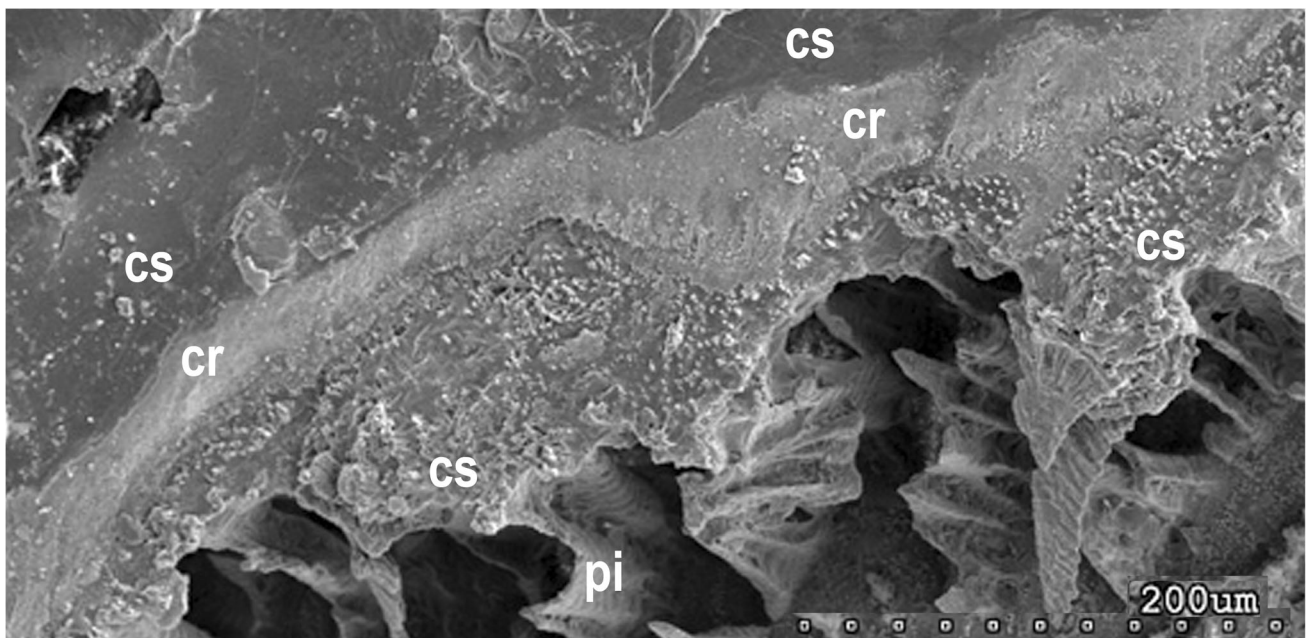

Fig. 2 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Ventral side of cuttlebone showing connecting stripes and contacting ridges of the siphonal zone. *Scale bar* is 1 mm. *cr* contacting ridge, *cs* connecting stripe, *pi* pillar structure

Fig. 3 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Ventral side of cuttlebone showing fractured connecting stripes attached to contacting ridges and microglobular structural units near contacting ridges. *Scale bar* is 500 μm. *cr* contacting ridge, *cs* connecting stripe, *g* globular crystalline units, *pi* pillar structure
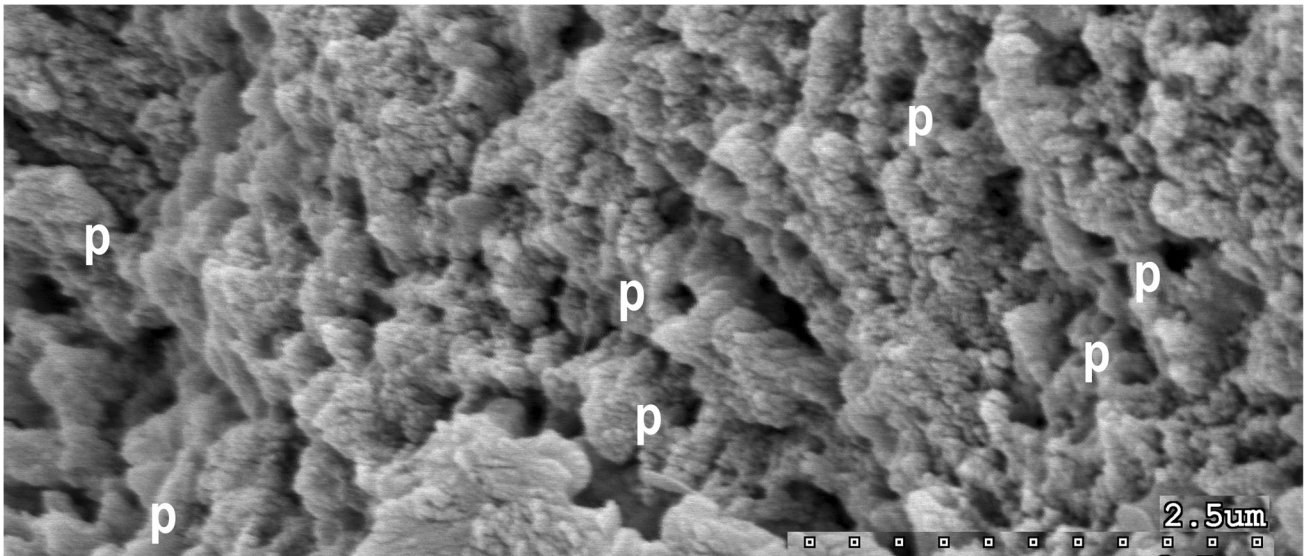

Fig. 4 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Ventral side of cuttlebone showing the contacting ridge (in the *middle*) and organic (*above* the ridge) and inorganic– organic (*below* the ridge) portions of two connecting stripes attached to the contacting ridge on both sides. *Scale bar* is 200 μm. *cr* contacting ridge, *cs* connecting stripe, *pi* pillar structure
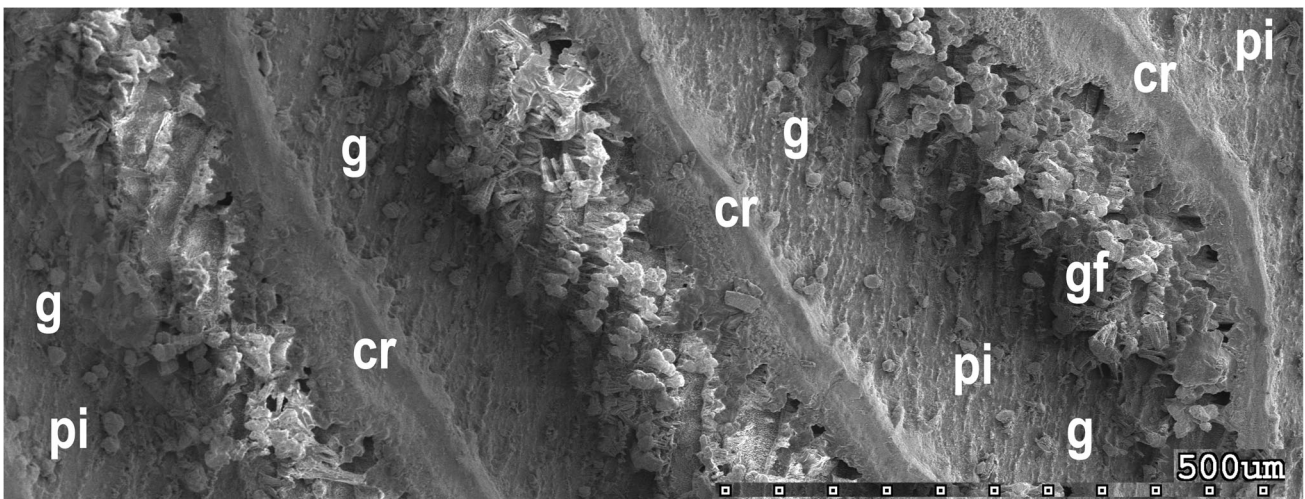
Contacting ridges

Contacting ridges are present on the adoral and the apical septal surfaces along septal edges (Figs. 1, 2, 3, 4, 6). Contacting ridges consist of globular crystalline units within an organic matrix; each globular crystalline unit is a stack of rounded, parallel to septal surfaces, alternating organic and mineralized microlaminas (Fig. 7). Mineralized microlaminas are formed by carbonate microgranules and have lamella–granular ultrastructure. The posterior and anterior slopes of the contacting ridge seem to have different mineralization (Figs. 3, 4). Contacting ridges have

Fig. 5 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Close up of Fig. 4, showing microporosity of the inorganic–organic portion of connecting stripe. *Scale bar* is 2.5 μm. *p* pore

Fig. 6 *Sepia officinalis*. Beach-collected cuttlebone; southern Portugal. Ventral side of cuttlebone showing the interstices between four succeeding contacting ridges filled with the microgranular material in siphonal zone. *Scale bar* is 500 μm. *cr* contacting ridge, *g* granular crystalline units, *gf* granular filing of "openings" of cameras, *pi* pillar structure

micro- and nannopores of about 0.1–0.01 μm in diameter and contain numerous interspaces filled with organic material between the mineralized globules.

Septa

Septa are thin, achoanitic, formed by lamella–fibrillar nacre. They are coated with a prismatic layer which is the basal part of the pillar structure (Fig. 8). Longitudinally fractured septa show fine laminas and course criss-cross pattern reflecting the different orientations of the short rod-like crystalline units of the overlapping laminas (Fig. 9).

Comparison of phragmocone structures in *Sepia* and *Spirula*

Despite remarkable morphological differences between the siphonal zone of *Sepia* and the fully developed tubular siphuncle of *Spirula,* there are striking similarities in their phragmocone structures. These include the narrow slit-like shape of permeable zones between chambers and the siphuncle (Figs. 1, 11, 12), and, additionally, the structural filling of the slit-like "openings" of chambers with granular or prismatic material as seen in *Sepia* (Fig. 6) and *Spirula* (Figs. 11, 12). Phragmocones with narrowed

Fig. 7 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Ventral side of cuttlebone showing three globular crystalline units in contacting ridge and their microlaminated ultrastructure. *Scale bar* is 50 µm. *cr* contacting ridge, *g* globular crystalline unit
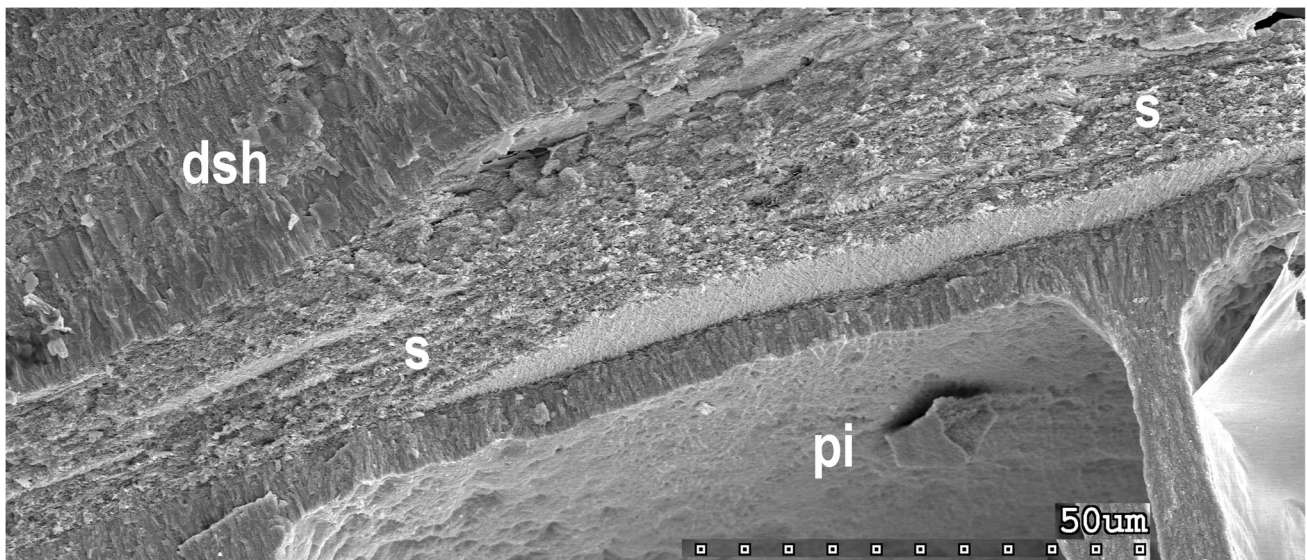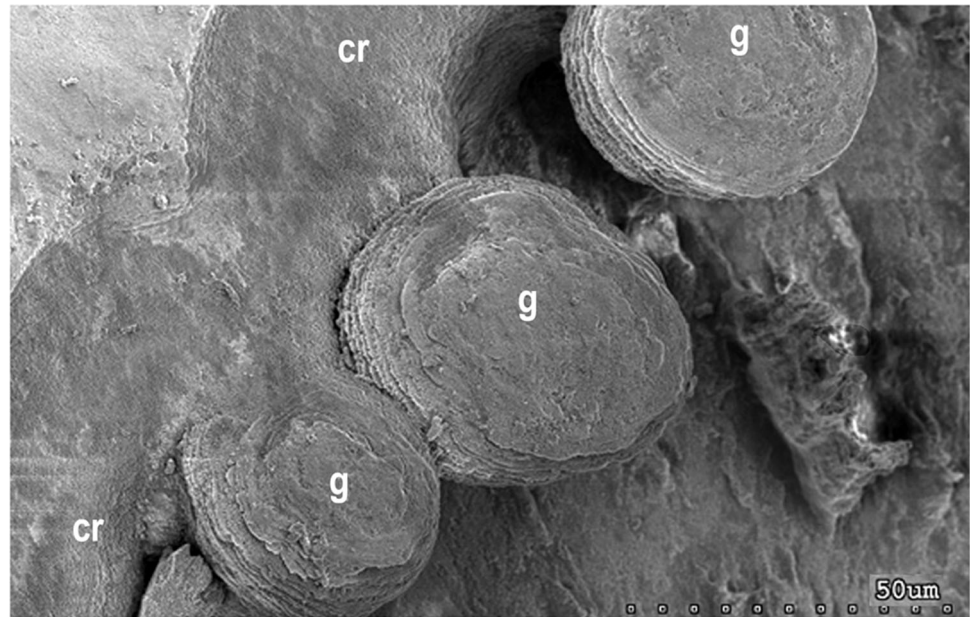
Fig. 8 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Longitudinal section of cuttlebone showing dorsal shield (*top*), mural part of septum (*middle*) and prismatic basal part of pillar structures in contact with laminated septum. *Scale bar* is 50 µm. *dsh* dorsal shield, *pi* pillar structure, *s* septum

permeable zones between chambers and the siphuncle (Figs. 6, 11, 12) may allow for increased resistance to high hydrostatic pressure and enable both genera to migrate to greater depths either seasonally or daily. However, in *Sepia,* the permeable "openings" between chambers and the siphuncle are long, approximately equal to the cuttlebone width (Figs. 1, 2); in *Spirula,* they are short, about the circumference length of the siphonal tube (Figs. 11, 12). The narrow but long porous permeable zones, as seen in *Sepia,* may contribute to rapid buoyancy regulation, and,

therefore, allow for environmental plasticity and higher species diversity. *Spirula* has relatively short permeable zones and may be less adaptable to rapid hydrostatic changes.

Lamella–fibrillar nacre in septa of *Sepia* and *Spirula* exhibits minor ultrastructural difference as well. In *Sepia,* each lamella consists of short fibre-like crystalline units, rather than long tread-like fibres observed in *Spirula* (compare Figs. 9, 10). This makes lamella–fibrillar nacre of septa in *Sepia* more similar to that of the middle Eocene

sepiid *Mississaepia* Weaver, Dockery III et Ciampaglio, 2010 (Doguzhaeva et al. 2014: Pl. 7, Figs a1–a5) than to *Spirula* (Fig. 10). Lamella–fibrillar nacre, observed in *Sepia*, *Mississaepia* and *Spirula*, exhibits a characteristic criss-cross pattern formed by different orientation of rod- or fibre-like ultrastructural elements in the overlapping lamellas (Fig. 10; Doguzhaeva et al. 2011: Fig. 1a).

The lamella–fibrillar nacre in septa of belemnites and fossil spirulids, has not yet been studied in detail, but is suggested by fine lamination and granular appearance of septal material in sections, as well as, the absence of columnar and plate-like structural elements (Doguzhaeva 1996: Pl. 6, Figs. 2, 4, 5; Doguzhaeva et al. 2003: Figs. 5, 6). Lamella–fibrillar nacre is the coleoid-related septum
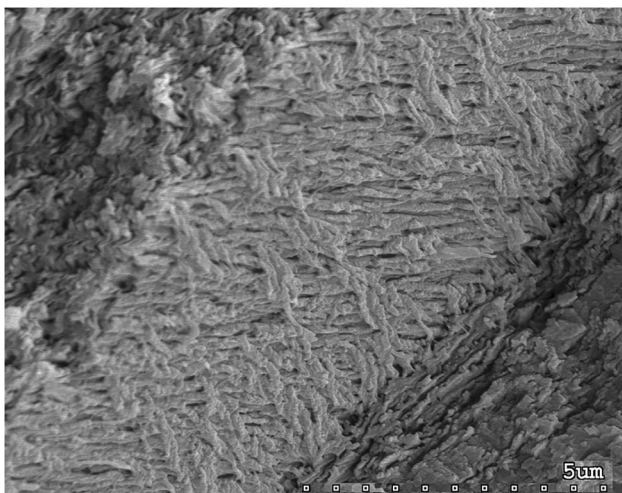
Fig. 9 *Sepia officinalis*. Beach-collected cuttlebone; Vale do Lobo, southern Portugal. Enlarged detail of Fig. 8. Fractured septum showing a *criss-cross pattern* of lamella–fibrillar nacre; note short rod-like crystalline units of overlapping laminas. *Scale bar* is 2 μm

ultrastructure currently documented in *Spirula* (Fig. 10), *Sepia* (Fig. 9), *Mississaepia* (Doguzhaeva et al. 2014: Pl. 7, Figs a1–a5) and some fossil spirulids and belemnoids (Doguzhaeva et al. 2011). It seems unlikely that this ultrastructure would appear independently in septa of *Sepia* if the cuttlebones originated from gladii by means of their secondary mineralization as is suggested by Bonnaud et al. (2006).

Septal necks are missing in *Sepia* while in *Spirula*, they are long (about camera length) retrochoanitic and leave deep attachment scars on shell wall (Doguzhaeva 2000: Pl. 1, Fig. 3; Pl. 2, Figs. 7, 8; Bandel and Stinnesbeck 2006: Pl. 3, Fig. 7; Fuchs et al. 2012: Fig. 9D).

## Discussion on siphonal zone structure and its functional implication

In siphonal zone of cuttlebones, connecting stripes coat the slit-like interstices between septa (Figs. 1, 2, 3). Similarly, in other cephalopods, connecting rings cover the interstices between septal necks in tubular siphuncles. Connecting stripes apparently have a similar function to connecting rings and serve as transport routes for cameral liquid in and out of chambers for buoyancy regulation. Because septal necks are missing in *Sepia*, the connecting stripes are attached to the septal edges by contacting ridges. Near contacting ridges, the peripheries of the connecting stripes are mineralized (Figs. 3, 4). Because the contacting ridges have lamella–globular ultrastructure (Fig. 7) and consist of organic rich, granular, porous material (Fig. 5), they may also function as transport routes for the cameral liquid.

Among extinct cephalopods, thin fibrous porous connecting rings, like the connecting stripes of *Sepia*, were
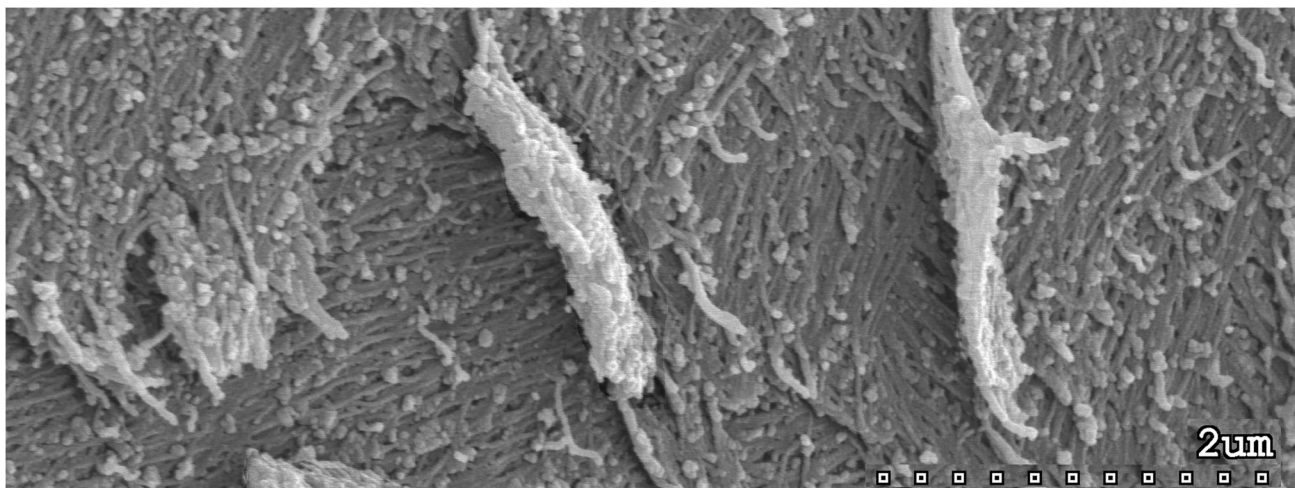
Fig. 10 *Spirula*. Beach-collected shell; Sydney, Ausralia. Lamella–fibrillar nacre of a septum. Fractured septum showing a *criss-cross pattern* indicative of lamella–fibrillar nacre; note closely spaced parallel fibres in two fractured overlapping laminas. *Scale bar* is 2 μm

revealed in exceptionally well preserved shells of the Early Cretaceous lythoceratid ammonoid *Eogaudryceras* (Spath 1927) (Doguzhaeva et al. 2010: Figs. 1, 2, 4, 7, 8, 9, 10). In this genus, like in other lythoceratids (Drushchitc and Doguzhaeva 1974, 1981; Doguzhaeva 1988), the tubular siphuncle shows features such as relatively small diameter, short permeable segments (connecting rings), long non-permeable segments (septal necks), and reinforced contacts between shell wall and septal necks, indicative of relatively high resistance to hydrostatic pressure (see also Westermann 1996). In *Eogaudryceras*, porous connecting rings apparently provided effective buoyancy regulation necessary for pelagic habitats, diurnal vertical migrations, and hovering or drifting in mid-water, as indicated by gross
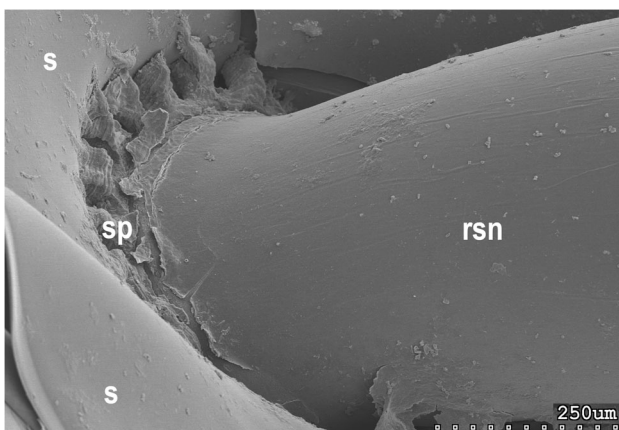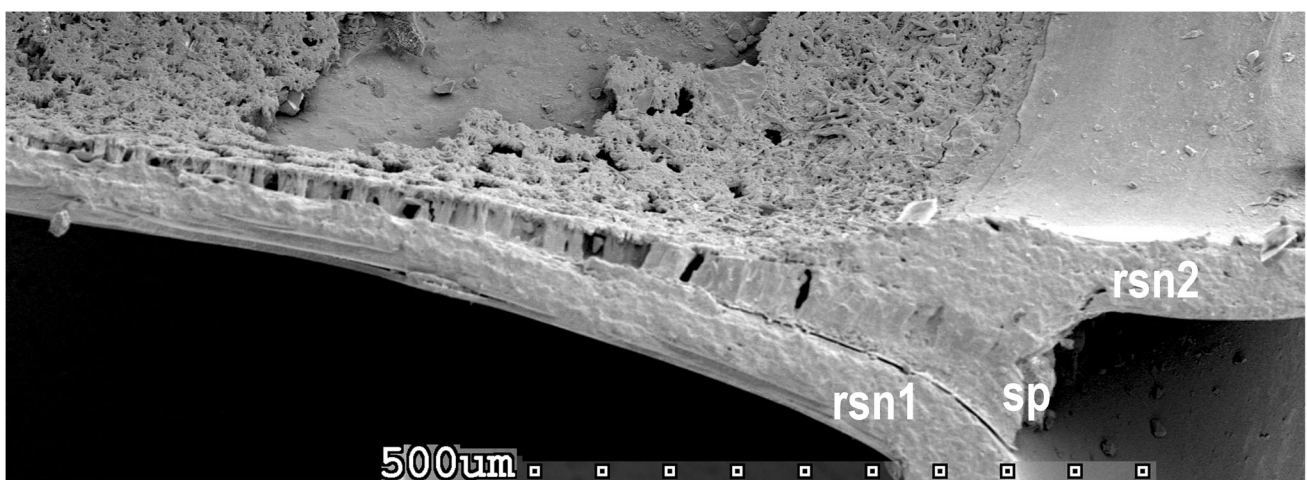
shell morphology (Doguzhaeva et al. 2010). Small-shelled *Eogaudryceras* apparently resembles, to some degree, the deep-water *Spirula* which also possesses narrow marginal siphonal tube, long septal necks, and short narrow permeable zones (Figs. 11, 12; Doguzhaeva 2000: Pl. 1, Figs. 1–3). Conversely, the non-porous connecting rings of siphonal tube in *Nautilus* (Mutvei et al. 2010) possess low permeability at a molecular level (Denton and Gilpin-Brown 1966) and provide slow, taking several days, evacuation of the cameral liquid. These factors allow *Nautilus* to exceed the depth of about 300 m for only short time (Ward and Boletzky 1984; Saunders and Ward 1987; Ward 1987; Greenwald and Ward 1987).

Long narrow porous connecting stripes and organic rich, loosely mineralized contacting ridges of the siphonal zone may provide effective buoyancy regulation by rapid evacuation of the cameral liquid in cuttlebones, and thus may enable the cuttlefishes to colonize a broad range of depths and different habitats. These basic factors allow for the environmental plasticity of sepiids and may explain high species diversity as demonstrated by more than a hundred known species (see Adam and Rees 1966; Khromov 1989; Khromov et al. 1998; Lu 1998; Reid et al. 2005; Aitken et al. 2005).

Conclusions

Microlaminated microporous band-like connecting stripes "sealing" the slit-like "openings" of chambers of the phragmocones, so far observed in *Sepia* (*Acanthosepion*) cf. *savignyi* and *S. officinalis* are presumably the universal structures of cuttlebones and are homologous to connecting

Fig. 11 *Spirula*. Beach-collected shell; Sydney, Ausralia. Slit-like permeable zone in tubular siphuncle with long retrochoanitic septal neck. *Scale bar* is 250 μm. *rsn* retrochoaniticseptal neck, *s* septum, *sp* slit-like permeable pillar zone

Fig. 12 *Spirula*. Beach-collected shell; Cuba. Median shell section through tubular siphuncle showing slit-like permeable zone filled with spherulitic-prismatic deposits of pillar zone between two retrochoanitic septal necks. *Scale bar* is 500 μm. *rsn1* and *rsn2* two neighbouring retrochoanitic septal necks, *sp* slit-like permeable zone between two septal necks filled with spherulitic-prismatic deposits of pillar zone

rings of tubular siphuncles in other cephalopods. In each chamber, the posterior edges of the connecting stripes are attached to the adoral septal surfaces and the anterior septal edges are attached to the adapical septal surface by contacting ridges. Contacting ridges consist of globular crystalline units within an organic matrix and have lamella–globular ultrastructure; each globular crystalline unit is a stack of rounded, alternating organic and mineralized microlaminas parallel to the septal surfaces. The mineralized microlaminas consist of carbonate microgranules and have a lamella–granular ultrastructure. Micro- and nanno-pores are of ca. 0.1–0.01 μm in diameter. Contacting ridges evidently strengthen the septum/connecting stripe contacts and reinforce the resistance of the cuttlebone to high hydrostatic pressure. Porous connecting stripes and loosely mineralized contacting ridges may serve as transport routes for cameral liquid in and out of the chambers for buoyancy regulation. The common feature of phragmocone structures in *Sepia* and *Spirula* is narrowed slit-like permeable zones between chambers and siphuncle; narrowing of the permeable zones supposedly provides shell resistance to hydrostatic pressure and capability for migration to deeper water of both genera. Long permeable zones in *Sepia* may promote rapid buoyancy regulation, possibly resulting in environmental plasticity and higher species diversity. In contrast, short narrow permeable zones in *Spirula* apparently provide only slow buoyancy regulation, which does not favour the environmental plasticity and higher species diversity. Septa of *Sepia* show lamella–fibrillar nacre; each lamella consists of short rod-like crystalline units, instead of long fibre-like ultrastructural elements in septa of *Spirula*. In this respect, lamella–fibrillar nacre of *Sepia* is more similar to lamella–fibrillar nacre seen in septum and septal neck of the Eocene sepiid *Mississaepia*. Presence of connecting stripes in cuttlebones of *Sepia,* which have morphological and ultrastructural similarities to connecting rings of ammonoids, and possibly of bactritoids and fossil coleoids, on the one hand, and lack the structures in gladii which might be transformed into connecting stripes in cuttlebones, on the other hand, do not support the hypothesized origin of cuttlebones by secondary mineralization of gladii (Bonnaud et al. 2006). Lamella–fibrillar nacre, known to be a coleoid-related shell ultrastructure and herein demonstrated in *Sepia* for the first time, refutes the idea of cuttlebones as a secondarily mineralized gladii (Bonnaud et al. 2006) as well.

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