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Respiratory structures in cornute stylophorans (Echinodermata)

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The diversity of ”accessory orifices” (sutural pores, cothurnopores, lamellipores) in cornute stylophorans is reviewed, based on detailed examination of both previously described and new material, to discuss their similarities and differences with the respiratory structures of other echinoderms. The orifices present in the most basal taxa (e.g. *Ceratocystis* and *Nevadaecystis*) are morphologically identical to the sutural pores of many other Cambrian echinoderms, therefore ruling out previous interpretations of these structures as multiple mouths, gonopores, and gill slits. The cothurnopores correspond to highly specialized covered sutural pores, each delimited by a pair of U-shaped plates. The large ”accessory orifices” of *Phyllocystis crassimarginata*, along with the morphologically identical but smaller ones observed in disjunct cothurnopores, are here designated as pustulipores; in life, they probably housed soft, papulae-like exothecal respiratory structures. The proto-lamellate organs correspond to dense aggregations of conjunct cothurnopores lacking pustulipores. The lamellate organs are reinterpreted as strongly folded structures, functionally analogous to pectinirhombs, composed of numerous, sutured lamellae, each consisting of a pair of tightly compressed U-shaped plates. There is no evidence to support the presence of a flap in cothurnopores, nor slit-like openings between the lamellae of lamellate organs. Similar respiratory structures (conjunct cothurnopores) are present in the type species of the two scotiaecystid genera *Thoralicystis* Chauvel, 1971 and *Proscotiaecystis* Ubaghs, 1994. Therefore, *Thoralicystis* is reinstated here as valid, while *Proscotiaecystis* is considered a junior synonym.

echinoderms | gill slits | respiration | stylophorans | sutural pores

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Introduction

In marked contrast with the condition in most other animal phyla, gas exchange in extant echinoderms can be achieved by a particularly wide variety of mechanisms, some of them implying highly specialized respiratory structures, such as the bursae of ophiuroids and the respiratory trees of holothuroids (Brusca et al., 2016). In most cases, however, gas exchange between seawater and internal body fluids occur directly across all parts of the body wall made of soft tissues, i.e. mainly the ambulacral tube feet (in all echinoderms), as well as protruding respiratory pouches or ”papulae” (in asteroids) (Shick, 1983; Brusca et al., 2016). This implies that, even within a same individual, different parts of its body wall may be involved in gas exchange.

The particularly abundant fossil record of echinoderms shows that the same phenomenon applied to the earliest known representatives of the phylum: Palaeozoic echinoderms display a particularly wide range of highly-specialized thecal structures, almost universally interpreted as involved in gas exchange. Epispires are probably the most widespread respiratory structures in Cambro-Ordovician echinoderms (Mooi et al., 2024). They were soft, papulate respiratory structures probably analogous to the papulae of extant asteroids, and associated with sutural pores, i.e. rounded to oval orifices located across the boundaries between two (or three) adjoining skeletal elements (Ubaghs, 1968a; Sprinkle, 1973). Epispires have been described in cinctans (e.g. *Trochocystites*; Ubaghs, 1971; Friedrich, 1993), edrioasteroid-like taxa (e.g. *Camptostroma*, *Stromatocystites*; Paul and Smith, 1984; Zamora et al., 2015), early crinoids (e.g. *Adelphicrinus*, *Titanocrinus*; Guensburg and Sprinkle, 2003; Guensburg et al., 2023), and gogiid eocrinoids (e.g. *Akadocrinus*, *Lichenoides*; Ubaghs, 1953, 1968a; Nohejlová and Fatka, 2016; Sheffield et al., 2022). Although highly specialized respiratory structures may occur in some Ordovician crinoids (e.g. goniospires; see Sprinkle, 1982), the extinct subphylum Blastozoa clearly exhibits the greatest morphological disparity in thecal structures associated with gas exchange (Sheffield et al., 2022).

Two main types of respiratory structures have been identified in blastozoans, but this classification can actually be applied to all echinoderms (Hudson, 1911, 1915; Paul, 1968, 1972). In endothecal respiratory structures, ambient seawater enters the theca through external pores (or slits), and gas exchange occurs in internal canals or cavities: ophiuroid bursae, parablastoid cataspires, hemicosmitoid cryptorhombs, blastoid hydrospires, and glyptocystitoid pectinirhombs are examples of endothecal respiratory structures (Paul, 1968, 1972; Sheffield et al., 2022). In exothecal respiratory structures, gas exchange occurs outside of the theca, either in non-mineralized pouches protruding from the test, or in internal canals filled with body fluids: epispires (see above), as well as aristocystitid and sphaeronitid diplopores, comarocystitid foerstepores, holocystitid humatipores, caryocystitid humatirhombs, and asteroid papulae are examples of exothecal respiratory structures (Paul, 1968, 1972; Sheffield et al., 2022). Although respiratory structures have long been used to define taxonomic groups within blastozoans (e.g. Diploporita and Rhombifera), phylogenetic analyses have

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suggested that they can occur in different clades (Nardin and Bohatý, 2013; Sheffield and Sumrall, 2019). Furthermore, different types of respiratory structures can coexist within the same taxon, as for example in the blastoid *Troosticrinus*, which has both endothecal coronal canals and exothecal hydrospires (Sumrall and Waters, 2012).

Morphologically diverse thecal structures (”accessory orifices” *sensu* Ubaghs, 1968b) occurring in cornute stylophorans (e.g. cothurnopores, lamellipores) have regularly been assigned a probable respiratory function (e.g. Spencer, 1938; Jefferies, 1968; Philip, 1979; Parsley, 1988; Ubaghs, 1991; Lefebvre and Vizcaïno, 1999; Smith, 2005). Cornutes (middle Cambrian–Late Ordovician) correspond to a paraphyletic assemblage grouping most of the earliest members of the class Stylophora (Jefferies and Prokop, 1972; Derstler, 1979; Cripps, 1991; Parsley, 1997; Lefebvre et al., 2022). Cornutes are characterized by the possession of a single feeding appendage (aulacophore) inserted to a flattened, asymmetrical theca (Fig. 1A) (Ubaghs, 1963, 1967, 1968b; Parsley, 1988; Lefebvre et al., 2019; Rahman and Zamora, 2024). Since cornutes show no sign of five fold symmetry, their phylogenetic position within, and even outside, echinoderms has long been debated (see e.g. Bather, 1913; Jaekel, 1918; Gislén, 1930; Ubaghs, 1963; Jefferies, 1968; Parsley, 1988; David et al., 2000; Smith, 2005; Zamora and Rahman, 2014; Lefebvre et al., 2019, 2024). While the description of exceptionally preserved remains of the ambulacral system in the cornute aulacophore has clarified the nature of their appendage (Lefebvre et al., 2019), the debate is still ongoing on the interpretation of their accessory orifices: do they correspond to gill slits homologous to those occurring in chordates and hemichordates (e.g. Gislén, 1930; Jefferies, 1968, 1986; Jollie, 1982; Smith, 2005, 2008; Bottjer et al., 2006) or to regular echinoderm respiratory structures (e.g. Spencer, 1938; Philip, 1979; Ubaghs, 1983, 1991, 1994; Parsley, 1988; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022)?

The main objective of this contribution is to review the diversity of accessory orifices in cornutes, based on the detailed examination of previously described and new material, in order to discuss their similarities and differences with other respiratory structures present in echinoderms. Such a sample-based approach is necessary, as highly contrasting descriptions of the same structures, leading to widely divergent interpretations, have been published in the literature. In this context, the priority is therefore to provide a set of fundamental and reproducible observations and descriptions.

Previous interpretations of cornute respiratory structures

Multiple mouths

Respiratory structures were first identified and described in detail by Bather (1913), from abundant material of *Cothurnocystis elizae* and *Scotiaecystis curvata*, both preserved in the relatively coarse-grained sandstones of the late Katian Threave Glen Formation of Scotland (UK). In the right corner of the upper thecal surface of *C. elizae*, he observed up to 15 distinct elliptical areas, each framed by a pair of opposite, unequal U-shaped plates surrounding a large, elongated thecal pore (Bather, 1913, 1926, 1930). Collapsed skeletal elements located within the U-shaped elements were interpreted as ambulacral cover plates (Fig. 2A). Therefore, Bather (1913) concluded that each pore was a mouth protected by alternating cover plates (Fig. 2A) (see also Bather, 1926, 1930; Thoral, 1935; Chauvel, 1941; Delpey, 1941).

Bather (1913) considered the wide pectinirhomb-like structure occupying the same position on the upper thecal surface of *Scotiaecystis* to be morphologically equivalent to the cluster of elliptical areas in *Cothurnocystis*. Each lamella of the rhombic organ of *S. curvata* was interpreted as a pair of highly compressed U-shaped plates (Bather, 1913). He therefore suggested that ambulacral cover plates were certainly present on the lamellae of *S. curvata* (Bather, 1913, 1926, 1930). Bather (1913) also discussed the probable affinities of the thecal pores of *Cothurnocystis* and *Scotiaecystis* with those present in the same position (right anterior corner of the supracentral area) in *Ceratocystis*.

Gonopores

Jaekel (1918) shared Bather’s (1913) opinion on the probable homology of the thecal pores of *Ceratocystis perneri*, *Cothurnocystis elizae* and *S. curvata*. However, he considered it highly unlikely that cornutes had multiple mouths. He suggested instead that all the structures located in the right anterior corner of their theca were more likely gonopores.

Gill slits

Based on Bather’s (1913) description of *C. elizae* and *S. curvata*, as well as on their asymmetrical location on the theca, Gislén (1930) was the first to suggest that these elongated thecal pores were gill slits, homologous to those present in chordates. This interpretation was further developed by Jefferies (1968), based on the extensive reexamination and redescription of the two cornutes from the Threave Glen Formation. In *C. elizae*, Jefferies (1968) confirmed the presence of collapsed skeletal elements within the pairs of U-shaped plates, and considered them to be part of a mobile flap articulated to the abmarginal (posterior) U-shaped element (Fig. 2B). Jefferies (1968) therefore suggested that the thecal pores of *C. elizae* were most likely branchial openings functioning as exhalent, outlet valves, as predicted by Gislén (1930).

The morphology of the large rhombic structure of *S. curvata* was described in detail by Jefferies (1968), who provided accurate reconstructions of its external and internal aspects (Fig. 3). In the absence of any orifice in this structure, Jefferies (1968) hypothesized that narrow slits might open along the sutures between adjacent lamellae, so that seawater could enter a supposed intrathecal pharynx. Jefferies (1968) therefore concluded that cornutes were calcichordates, i.e. basal chordates possessing gill slits and an echinoderm-like calcite endoskeleton. Similarly to Bather (1913) and Jaekel (1918), Jefferies (1969, 1986) suggested that the thecal pores of *Ceratocystis* were most likely homologous to those of *Cothurnocystis* and *Scotiaecystis*. Jefferies’ (1968, 1969, 1986) interpretation of cornute thecal structures as branchial openings homologous to those occurring in chordates and hemichordates has been widely followed in the literature (see e.g. Bönik et al., 1978; Jollie, 1982; Cripps, 1988; Daley, 1992; Woods and Jefferies, 1992; Gil Cid et al., 1996; Gee, 2001; Smith, 2005, 2008; Bottjer et al., 2006).

Respiratory structures

Based on Bather’s (1913) description of the thecal pores in *C. elizae* and *S. curvata*, Spencer (1938) rejected interpretations that they were multiple mouths (Bather, 1913, 1926, 1930), gonopores (Jaekel, 1938), and gill openings (Gislén, 1930). Instead, Spencer

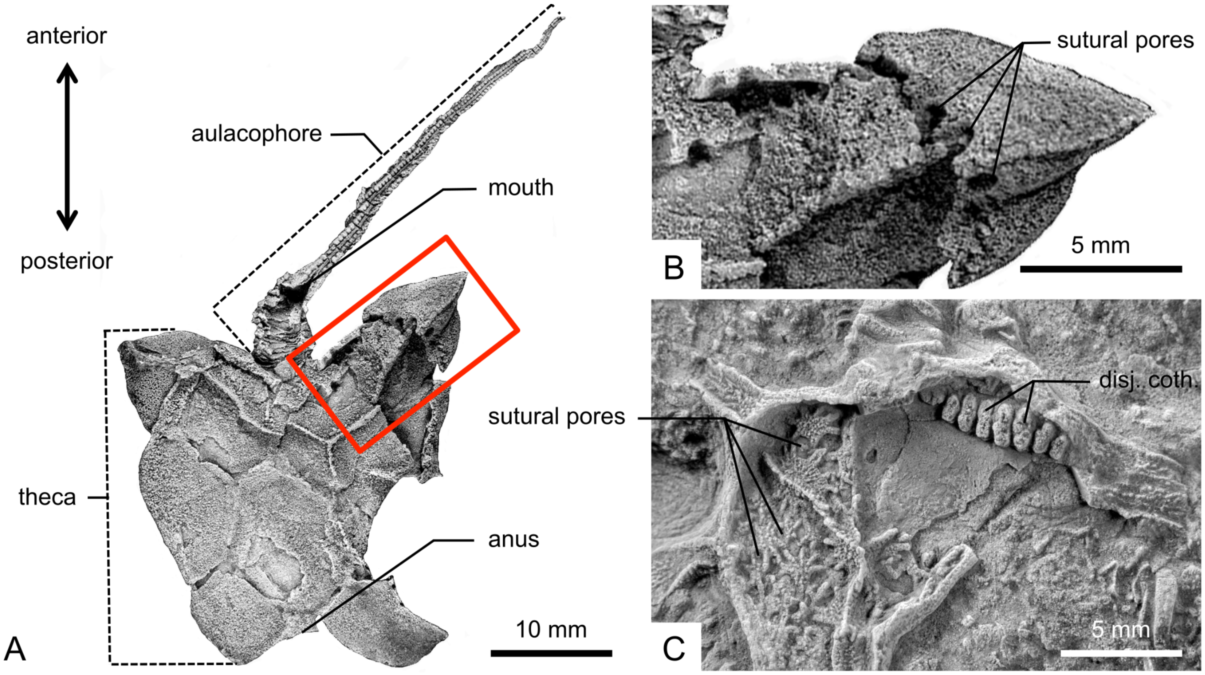

Figure 1. Cornute morphology and respiratory structures. (**A–B**). *Ceratocystis perneri*, NMP.L.10392, lectotype, Buchava Formation (Drumian, Cambrian), Skryje-Týřovice Basin, Czech Republic; latex cast of original specimen. (**A**) Morphology of the theca and the aulacophore, in upper aspect; the red box indicates the location of (B). (**B**) Right anterior corner of the upper thecal surface, with sutural pores. (**C**) *Nevadaecystis americana*, USNM.143237, holotype, Whipple Cave Formation (Cambrian Stage 10), Nevada, USA; original specimen. Upper thecal surface, with two types of respiratory structures: large sutural pores along the margins of stellate supracentrals (on the left), and disjunct cothurnopores (right anterior corner). Abbreviation: disj. coth., disjunct cothurnopores.

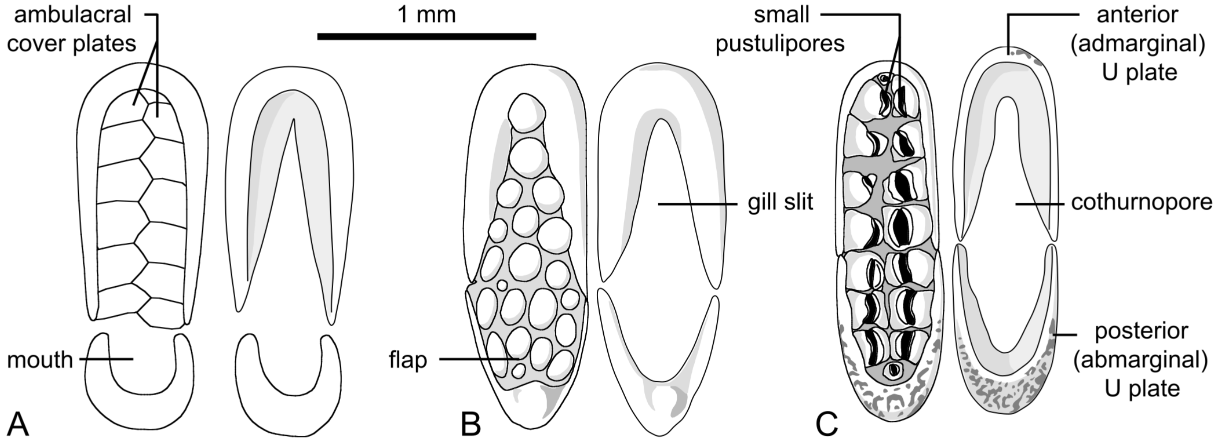

Figure 2. Main interpretations proposed for disjunct cothurnopores. (**A–B**) *Cothurnocystis elizae*, Threave Glen Formation (Katian, Lower Ordovician), Scotland, UK. (**A**) Disjunct cothurnopores as multiple mouths, partly covered by ambulacral cover plates. Redrawn and modified from Bather (1913). (**B**) Disjunct cothurnopores as outlet valves (gill slits), protected by a mobile flap. Redrawn and modified from Jefferies (1968). (**C**) *Phyllocystis blayaci*, Saint-Chinian Formation (Tremadocian, Lower Ordovician), Montagne Noire, France. Disjunct cothurnopores covered by specialized integumentary platelets forming two rows of pustulipores. Redrawn and modified from Ubaghs (1969).

(1938) was the first to suggest that they were more likely respiratory structures, analogous to those known in many other groups of Palaeozoic echinoderms (e.g. diplopores, hydrospires, rhombs).

Ubaghs (1963, 1967, 1968b, 1969) provided numerous detailed descriptions of all types of body openings present on the upper thecal surface of cornutes. He coined the terms ”cothurnopores” for elongated body openings surrounded by a pair of opposite U-shaped plates (e.g. in *Cothurnocystis*, *Chauvelicystis*, *Nevadaecystis* and *Phyllocystis blayaci*) (Fig. 2C), and ”lamellipores” for the numerous slit-like openings separated by narrow calcite lamellae in scotiaecystids. All other large circular thecal orifices located at the junction between two or more plates (e.g. in *Ceratocystis* and *Phyllocystis crassimarginata*) were designated ”sutural pores” by analogy with other Palaeozoic echinoderms. Ubaghs (1963, 1967, 1968b, 1969) considered the cornute thecal pores to be associated with ”porous organs” of unknown function (see also Chauvel, 1966, 1971). Only Bather's (1913) ”multiple mouths” interpretation was clearly rejected by Ubaghs (1963, 1967, 1968b, 1969), who identified the aulacophore as a feeding structure bearing a single ambulacral ray and the mouth.

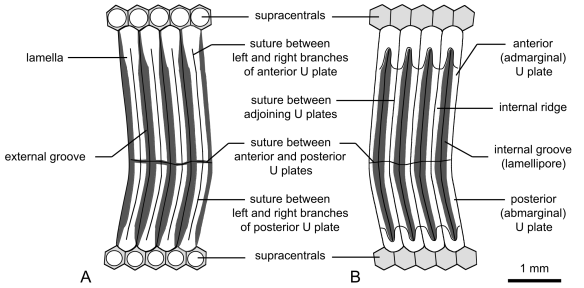

Figure 3. Respiratory structures in cornutes: partial reconstruction of the lamellate organ of *Scotiaecystis curvata*, Threave Glen Formation (Katian, Ordovician), Scotland, UK. Redrawn and modified from Jefferies (1968). (**A**) External aspect; each lamella corresponds to a pair of opposite (closed) U-shaped plates. Lamellae are separated by deep grooves. (**B**) Internal aspect; the internal ridges correspond to the external grooves, while internal grooves (lamellipores) occur within each pair of opposite U-shaped plates (external lamellae).

Spencer's (1938) suggestion that cornute "accessory orifices" might be respiratory structures analogous to sutural pores or pectinirhombs was taken up by Philip (1979), and subsequently followed in several contributions (see e.g. Parsley, 1988, 1997; Ubaghs, 1991, 1994; Lefebvre and Vizcaïno, 1999; Lefebvre, 2003; Lefebvre et al., 2022; Jackson, 2024).

Materials and methods

Material and institutional abbreviations

The observation of respiratory structures (when present), was carried out on all available specimens of cornutes deposited in the collections of the Cadi-Ayyad University, Marrakech, Morocco (AA), the Natural History Museum, London, UK (BMNHUK), the Czech Geological Survey, Prague, Czech Republic (CGS), the Universidad Nacional de Jujuy, San Salvador de Jujuy, Argentina (UNJu), Géosciences Rennes, Rennes, France (IGR), the Musée du Biterrois, Béziers, France (MB), the Museo Geominero, Spanish Geological Survey, Madrid, Spain (MGM), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), the Muséum d'Histoire Naturelle de Marseille, Marseille, France (MHNM), the Muséum d'Histoire Naturelle de Nantes, Nantes, France (MHNN), the Muséum d'Histoire Naturelle de Toulouse, Toulouse, France (MHNT), the Musée des Confluences, Lyon, France (ML), the Naturhistorisches Museum, Vienna, Austria (NHMW), the Národní Muzeum, Prague, Czech Republic (NMP), the National Museum of Wales, Cardiff, UK (NMW), the Naturhistoriska Riksmuseet, Stockholm (NRS), the Université Claude Bernard Lyon 1, Villeurbanne, France (UCBL-FSL), the Université de Montpellier, Montpellier, France (UM), and the United States Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

This material represents over 2,000 specimens comprising the type series of most cornute taxa described in the Czech Republic (*Bohemiaecystis bouceki*, *Ceratocystis perneri*, *Destombesicarpus budili*, *Hanusia obtusa*, *H. prilepensis*, *H. sarkensis*, *Prokopicystis mergli*, *Reticulocarpos hanusi*, *Thoralicarpus prokopi*), France (*Ampelocarpus landeyranensis*, *Amygdalotheca griffei*, *Arauricystis occitana*, *A. primaeva*, *Bohemiaecystis griffei*, *B. ubaghsi*, *Ceratocystis vizcainoi*, *Chauvelicystis spinosa*, *C. vizcainoi*, *Domfrontia pissotensis*, *Galliaecystis lignieresi*, *G. ubaghsi*, *Lobocarpus vizcainoi*, *Lyricocarpus courtessolei*, *Milonicystis kerfornei*, *Nanocarpus dolambii*, *Persiacarpos fellinensis*, *Phyllocystis blayaci*, *P. crassimarginata*, *Procothurnocystis courtessolei*, "*Proscotiaecystis*" *melchiori*, *Thoralicarpus guilloui*, *Trigonocarpus singularis*), Morocco (*Arauricystis clariondi*, *Bohemiaecystis chouberti*, "*B.*" *zagoraensis*, *Chauvelicystis ubaghsi*, *Destombesicarpus izegguirenensis*, *Domfrontia milnerorum*, *Milonicystis reboulorum*, *Thoralicarpus bounemrouensis*), Spain (*Thoralicarpus jefferiesi*), the United Kingdom (*Cothurnocystis elizae*, *Flabellicarpus rushtoni*, *Prochauvelicystis semispinosa*, *Procothurnocystis owensi*, *Protocystites menevensis*, *Scotiaecystis collapsa*, *S. curvata*), and the United States of America (*Nevadaecystis americana*), as well as numerous yet undescribed taxa.

Methods

Except for the holotype of *Nevadaecystis americana* (Fig. 1C), which is preserved in original calcite, all other observed and measured specimens occur as imprints in the rock. They therefore had to be casted with latex, so as to reveal their original, three-dimensional morphology. For observation and photography, latex casts were coated with ammonium chloride (NH_4Cl). The holotype of *N. americana* was observed dry, under water, and under ethanol. All photographs were taken with a Canon 5DSR camera equipped with a MP-E 65 or 100 mm macro lens.

Terminology and orientation

The orientation (with the aulacophore considered anterior and the theca, posterior) follows Ubaghs (1963, 1968b, 1969), in accordance with the identification of exceptionally preserved soft parts in the appendage of cornutes, which corroborates its identification as a feeding (and locomotory) device bearing a single ambulacral ray and the mouth (Lefebvre et al., 2019). The lower thecal surface of cornutes often has protuberances (knobs, spikes), which probably served as anchoring structures on soft substrates (Lefebvre, 2003). All presumed respiratory structures are systematically located on the opposite (upper) thecal surface. The morphological terminology follows closely that used in the *Treatise of Invertebrate Paleontology* (Ubaghs, 1968b), and its updates (e.g. Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). The plate terminology and presumed homologies are based on Lefebvre et al. (2022).

Results

Detailed examination of hundreds of specimens belonging to over 50 different cornute taxa confirms the presence of external thecal structures generally interpreted as associated with a respiratory function (sutural pores, cothurnopores, lamellate organs) in most of them, but also their absence in several taxa (Table 1). The observation of new and better-preserved specimens of *Milonicystis*, amygdalothecids (*Amygdalotheca*, *Domfrontia*, and *Nanocarpus*), and most hanusiids (*Galliaecystis*, *Hanusia*, *Prokopicystis*, *Reticulocarpos*) demonstrates that all gaps and putative orifices assumed to be present in the right anterior corner of their supracentral area (see e.g. Jefferies and Prokop, 1972; Cripps, 1989a, b; Cripps and Daley, 1994) correspond to taphonomic artefacts, i.e. to disarticulated and/or broken plates (see Ubaghs, 1994). In most cases, doubt was permitted when only a handful of incomplete specimens were available, as in the case of *Amygdalotheca griffei*, initially described from two individuals from the late Tremadocian of the Montagne Noire, France (Ubaghs, 1969). In the last years, coeval levels from the Fezouata Formation in Morocco yielded dozens of fully articulated specimens of *A. griffei* (Lefebvre et al., 2016). Examination of this abundant and well-preserved material confirms

Table 1. Morphological terminology and associated species

Respiratory Structures	Description	Cornute Taxa
Sutural pores	Relatively large, rounded to slightly elliptical thecal orifices distributed along plate sutures	*Ceratocystis, Nevadaecystis, Protocystites*
Pustulipores	Small thecal orifices opening at the apex of truncated cones constructed by the upturned edges of several supracentrals	*Phyllocystis crassimarginata*
Disjunct cothurnopores	Relatively large, rounded to elliptical thecal orifices opening at the suture between two opposite U-shaped plates, and covered with a thin layer of integument pierced by one or two longitudinal series of minute pustulipores; U-shaped plates of neighbouring cothurnopores not in contact with each other	*Acuticarpus, Archaeocothurnus, Chauvelicystis, Cothurnocystis, Drepanocarpos, Nevadaecystis, Persiacarpos, Phyllocystis blayaci, Ponticulocarpus, Prochauvelicystis*
Conjunct cothurnopores	Relatively narrow and elongate thecal orifices opening at the suture between two opposite U-shaped plates, and covered with a thin layer of integument without pustulipores; U-shaped plates of neighbouring cothurnopores tightly sutured to each other along their lateral margins, and together forming a proto-lamellate organ	*Flabellicarpus, Thoralicystis*
Lamellipores	Slit-like thecal orifices opening internally at the base of hollow, closed lamellae formed by laterally strongly compressed, opposite U-shaped plates; U-shaped plates of neighbouring cothurnopores tightly sutured to each other along their lateral margins, and together forming a lamellate organ	*Bohemiaecystis, Scotiaecystis, Thoralicarpus*
No respiratory structures	No thecal respiratory structures	*Ampelocarpus, Amygdalotheca, Destombesicarpus, Domfrontia, Galliaecystis, Hanusia, Milonicystis, Nanocarpus, Prokopicystis, Reticulocarpos, Sokkaejaecystis*

the absence of any respiratory structure in this taxon (Ubaghs, 1969). Respiratory structures are also absent in small-sized chauvelicystids (*Ampelocarpus*, *Destombesicarpus*, *Lyricocarpus*, *Sokkaejaecystis*) and in some cothurnocystids (e.g. *Arauricystis occitana* and a yet undescribed *Procothurnocystis* from the Fezouata Formation) (Ubaghs, 1994; Lefebvre et al., 2022).

Sutural pores

The preserved left and central parts of the upper thecal surface of the holotype and only known specimen of *Nevadaecystis americana* (Whipple Cave Formation, Cambrian Stage 10; Nevada, USA) consist of numerous, large, stellate, thin supracentrals, ornamented with small granules and low radiating ridges (Fig. 1C). Large, rounded to elliptical pores (i.e. actual openings through the plating of the upper thecal surface) are shared between neighbouring supracentrals. As all of these pores are occurring across the sutures between adjacent plates, they fit the definition of sutural pores proposed for early Palaeozoic echinoderms (see e.g. Ubaghs, 1968a; Sprinkle, 1973; Sheffield et al., 2022). The pattern observed in *Nevadaecystis*, with numerous large sutural pores widely distributed over the supracentral integument, is unique among cornutes.

The heavily plated primitive cornute *Ceratocystis perneri* (Buchava and Jince formations, Drumian; Skryje-Týřovice and Jince Basins, Czech Republic) is characterized by the presence of a single series of relatively large, rounded to elliptical orifices occurring across the sutures between three broad skeletal elements forming the right anterior corner of the theca (A_1, M_2 and M_3) and the three plates inserted above (A_0, *Mc* and *Ms*) (Figs. 1B, 4A). The number of pores is variable and ranges from 12 to 15. To the left of the aulacophore insertion, an additional pore of similar shape is also present on the opposite (lower) side of the theca, across the suture between A_1' and M_1'. The diameter of these openings is variable within a same individual, and generally ranges from 0.6 to 2 mm (maximum length), and from 0.3 to 0.5 mm (maximum width). The upper (outer) margin of pores is sometimes outlined by a faint ridge, while their lower (inner) edge is always smooth. Pores are widely open, and no plates or integument have been observed above or within them. Morphologically similar orifices, identically distributed over the theca are also present in all other examined *Ceratocystis* specimens from the Drumian of France, Morocco, Spain, and Sweden, as well as, very likely, in the strongly tectonically distorted and closely related primitive cornute *Protocystites menevensis* (Saint David's Series, Drumian; Wales, UK). In all these taxa, the orifices are consistently restricted to a narrow crescent-shaped region in the right corner of the upper thecal surface. Moreover, as they are always distributed across two (or three) adjacent plate sutures, they correspond very closely to the definition of "sutural pores".

Pustulipores

The right anterior corner of the upper thecal surface of *Phyllocystis crassimarginata* (Saint-Chinian Formation, late Tremadocian; Montagne Noire, France) is perforated with numerous orifices (0.3 to 0.6 mm wide), each opening at the apex of a small truncated cone or pustule constructed by the upturned edges of several (two to five) supracentrals (Figs. 4B, 5E). Some of these modified supracentrals may be involved in the walls of two or more cones. Pores are more or less rounded to quadrangular in outline. Their number increases with growth, ranging from about 15 in the smallest individuals to more than 50 in the largest ones. In smaller specimens, their distribution appears relatively random within a crescent-shaped area extending mainly along the abmarginal edges of M_2 and *Mc*. In larger individuals, pores tend to be aligned and form about a dozen more or less regular rows, roughly perpendicular to the marginal frame (Fig. 5F, G). While the external surface of surrounding supracentrals is smooth, lateral walls of skeletal elements involved in the pore-bearing cones are characterized by granular ornamentation.

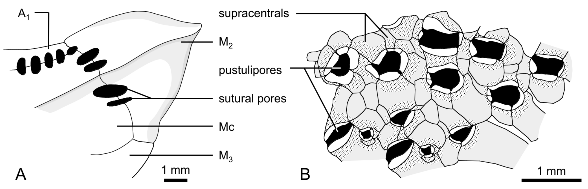

Figure 4. Respiratory structures in cornutes: sutural pores (A) and pustulipores (B). (**A**) *Ceratocystis perneri*, Buchava and Jince formations (Drumian, Cambrian), Jince and Skryje-Týřovice Basins, Czech Republic; sutural pores in the right anterior corner of the upper thecal surface. Redrawn and modified after Ubaghs (1967). (**B**) *Phyllocystis crassimarginata*, Saint-Chinian Formation (Tremadocian, Lower Ordovician), Montagne Noire, France; large pustulipores in the right anterior corner of the supracentral area. Redrawn and modified after Ubaghs (1969).

In contrast, the pore lips and the inner walls of the cones are both completely smooth.

The existence of such pores opening directly through the supracentral area, at the top of large, numerous, multi-plated chimneys or volcanoes is unique to *P. crassimarginata*. Because these pores open at the suture between several skeletal elements, Ubaghs (1968b, 1969) proposed to call them ”sutural pores”. However, comparison of the body openings of *P. crassimarginata* with the sutural pores of other Early Palaeozoic echinoderms (including *Ceratocystis* and *Nevadaecystis*; see above) highlights some differences. Sutural pores are usually located across the sutures between two (sometimes three) relatively thick skeletal elements (Ubaghs, 1968a; Sprinkle, 1973; Sheffield et al., 2022). They can be slightly depressed and/or surrounded by a low, rounded to elliptical ridge, but they never occur atop a truncated, raised chimney. In contrast, the walls of the pore-bearing cones in *P. crassimarginata* consist of an irregular number of thin, convex, and apparently unorganized platelets. Furthermore, the secondary alignment of these cones in larger individuals has no counterpart in echinoderms with sutural pores. For these reasons, the pore structures of *P. crassimarginata* are herein designated ”pustulipores”, to clearly differentiate them from the sutural pores found in other cornutes and echinoderms.

Disjunct cothurnopores

Following Ubaghs’ (1968b) original definition, cothurnopores correspond to elongated thecal orifices opening at the suture between two opposite U-shaped plates. The term ”disjunct cothurnopores” is proposed here for relatively large, elliptical cothurnopores clearly separated from each other by regular supracentral plates, comparable in size and morphology to those present elsewhere on the upper thecal surface (Fig. 5A-D). Disjunct cothurnopores are probably the most widespread type of pore structures in cornutes (Table 1). They are found in some of their earliest known representatives (e.g. *Ponticulocarpus robisoni* from the Wuliuan Spence Shale of Utah, USA, and *Archaeocothurnus bifida* from the Drumian Wheeler Shale of Utah, USA), in *Nevadaecystis americana* (Fig. 1C), several chauvelicystids (e.g. *Chauvelicystis*, *Prochauvelicystis*), most cothurnocystids (e.g. *Cothurnocystis*), basal-most hanusiids (e.g. *Drenanocarpos*), and *Phyllocystis blayaci* (Fig. 5C, D) (Saint-Chinian Formation, late Tremadocian; Montagne Noire, France).

The number of disjunct cothurnopores increases with growth and thecal size. It varies from three to four openings (e.g. *Prochauvelicystis semispinosa* from the late Tremadocian Shineton Shale; Shropshire, UK) to over 15 (e.g. *Cothurnocystis elizae*). The distribution of disjunct cothurnopores is always restricted to a crescent- to rhombic-shaped area located in the right anterior corner of the upper thecal surface (Fig. 5A, C). In a single individual, the first disjunct cothurnopores formed are located in the middle of this elongated region, while later and smaller openings are added at both ends. Disjunct cothurnopores and their associated U-shaped plates form relatively narrow, elliptical structures, all more or less perpendicular to the right anterior margin of the thecal frame.

The two U-shaped plates framing each disjunct cothurnopore have relatively high, often coarse, granular outer walls, and more gently sloping, smooth inner walls. These U-shaped plates are approximately similar in length (e.g. *Procothurnocystis owensi* from the Dapingian Pontyfenni Formation; Wales, UK; Fig. 5B). In some other taxa, the anterior (admarginal) U-shaped elements may be either slightly longer (e.g. *Nevadaecystis americana*, *Phyllocystis blayaci*; Figs. 1C, 5D), or shorter than the posterior (abmarginal) plates (e.g. *Chauvelicystis ubaghsi*, Fezouata Shale, Floian; Anti-Atlas, Morocco). Depending on the taxa, U-shaped plates may be narrow, with sharp upper edges (e.g. *Phyllocystis blayaci*; Fig. 5D) or broader, with thicker lateral walls (e.g. *Procothurnocystis owensi*; Fig. 5A). The posterior end of the abmarginal U-shaped element may sometimes be elongated into a spike-like process (e.g. *Persiacarpos? fellinensis* from the late Tremadocian Saint-Chinian Formation; Montagne Noire, France; see Ubaghs, 1969, fig. 20.2).

In many specimens, the original presence of disjunct cothurnopores can only be inferred from the preservation of their associated U-shaped plates, which are often collapsed, displaced, and no longer sutured to each other. In better-preserved individuals, numerous fragments of platelets can usually be observed within the U-shaped plates (Figs. 1C, 5B). However, in most cases, the precise arrangement and morphology of these small skeletal elements remain difficult to assess with accuracy, particularly when specimens are preserved in coarse-grained lithologies, as is the case, for example, in the Threave Glen Formation in Scotland, UK (*Cothurnocystis elizae*), or in the Izegguirene Formation, in the Anti-Atlas, Morocco (*Arauricystis clariondi*). Rare examples of almost pristine preservation make it possible to document the detailed morphology of disjunct cothurnopores and associated skeletal elements (Fig. 5D). In these exceptionally preserved specimens, the elongate orifices surrounded by opposite U-shaped plates are completely filled by a pavement of numerous, small skeletal elements forming one (e.g. cornute indet. from the latest Cambrian–early Tremadocian Dongjeom Formation; Taekaeksan Basin, Korea; Lee et al., 2005, fig. 3.4) or two longitudinal rows of small truncated cones, all with a tiny orifice at the apex (e.g. *Phyllocystis blayaci*; Fig. 5D). Each pore is longitudinally elongate and framed by the delicate lips of the two opposite convex platelets forming the lateral walls of the cone. The overall morphology of the numerous, small pore-bearing cones tightly packed in U-shaped plates (Fig. 5D) is remarkably similar to that of the 20–30 times larger isolated pustulipores of *Phyllocystis crassimarginata* (Figs. 4B, 5D, F).

In summary, the observation of particularly well-preserved disjunct cothurnopores demonstrates that these orifices did not open onto ambient seawater, but onto a small external elliptical cavity surrounded by two massive opposite U-shaped plates and overlain by a thin layer of integument (Fig. 5D). This integument was pierced by one or two longitudinal series of tiny pustulipores, morphologically identical to the larger ones present in *P. crassimarginata*.

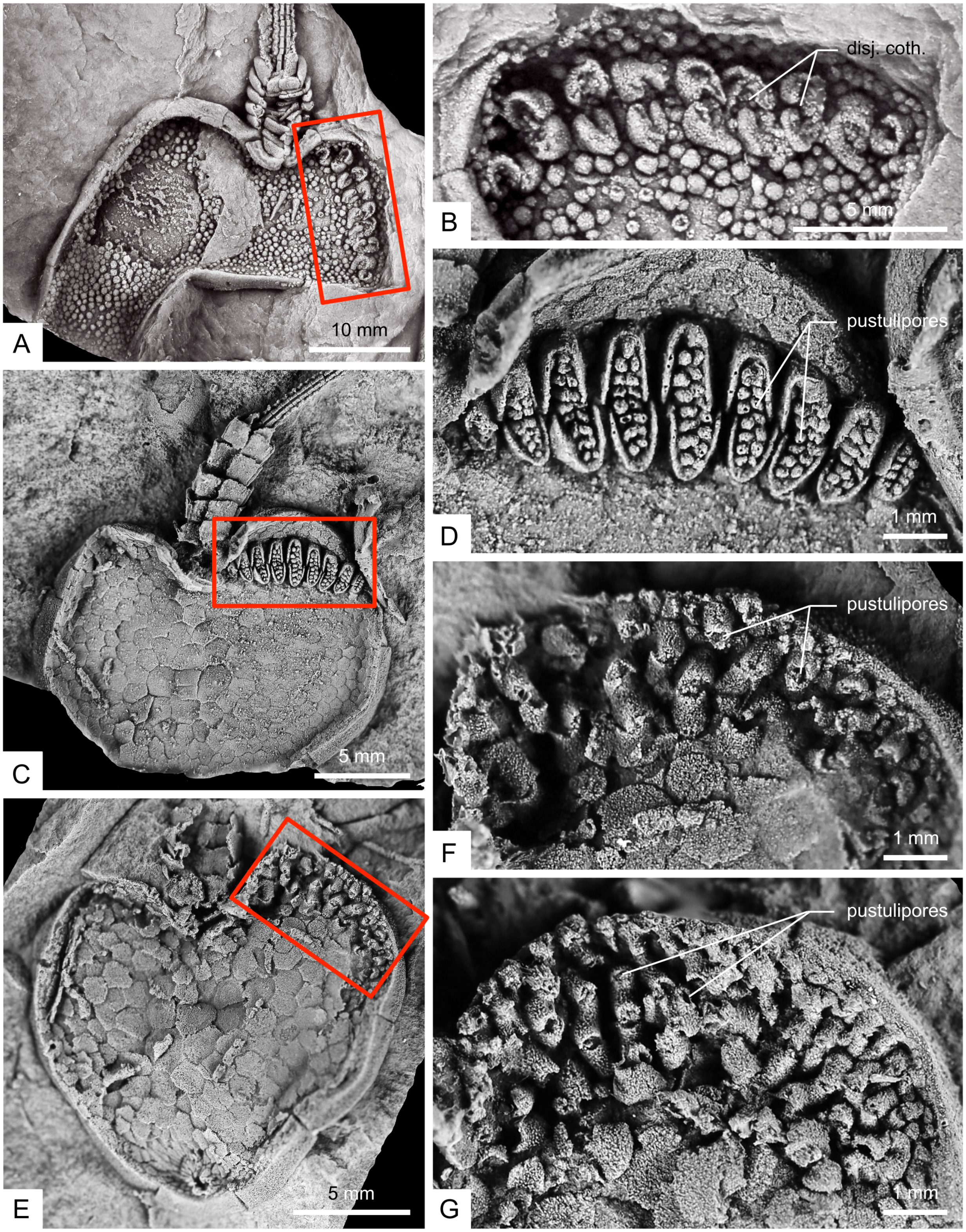

Figure 5. Respiratory structures in cornutes: disjunct cothurnopores (A–D) and pustulipores (E–G); latex casts of original specimens. (**A–B**) *Procothurnocystis owensi*, NMW.84.176.119, holotype, Pontyfenni Formation (Dapingian, Middle Ordovician), Wales, UK. (**A**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (B). (**B**) Disjunct cothurnopores in the right anterior corner of the theca, with undifferentiated, pustulose supracentrals inserted between them; small pustulipores are visible inside some pairs of opposite U-shapes plates. (**C–D**) *Phyllocystis blayaci*, IGR.114938, Saint-Chinian Formation (Tremadocian, Lower Ordovician), Montagne Noire, France. (**C**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (D). (**D**) Nine large disjunct cothurnopores in the right anterior corner of the supracentral area; two rows of small pustulipores are preserved inside each pair of opposite U-shaped plates. (**E–G**) *Phyllocystis crassimarginata*, Saint-Chinian Formation (Tremadocian, Lower Ordovician), Montagne Noire, France. (**E–F**) UCBL-FSL.712646. (**E**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (F). (**F**) Numerous, aligned, large pustulipores in the right anterior corner of the supracentral area. (**G**) UCBL-FSL.712618; numerous, aligned, large pustulipores in the right anterior corner of the upper thecal surface. Abbreviation: disj. coth., disjunct cothurnopores.

Conjunct cothurnopores

The right anterior corner of the upper thecal surface of ”*Proscotiaecystis*” *melchiori* (Landeyran Formation, late Floian; Montagne Noire, France) bears more than 20 very narrow, elongate, slit-like cothurnopores framed by closely packed pairs of opposite U-shaped plates (Figs. 6A-E, 7). Together, they form a long, slightly arched, crescent-shaped structure or ”proto-lamellate organ” (Lefebvre et al., 2017, 2022) roughly parallel to the abmarginal edges of M_1, *Mc* and M_3. The U-shaped plates are relatively low and decrease rapidly in size at both ends of the proto-lamellate organ (Figs. 6A-E, 7). Unlike the plate configuration seen in other cornutes with disjunct cothurnopores (see above), the pairs of U-shaped elements are not separated by supracentrals, but their lateral margins are tightly sutured. The term ”conjunct cothurnopores” is proposed herein for densely packed, adjoining cothurnopores, whose U-shaped plates are laterally sutured to each other.

The presence of small plates collapsed within the narrow elliptical slits surrounded by U-shaped plates suggests that conjunct cothurnopores did not communicate directly with the ambient environment, but were covered by a thin layer of delicate platelets (Fig. 7). None of the observed specimens of *”P.” melchiori* shows any evidence suggesting the presence of small pustulipores. All platelets occurring within slit-like U-shaped elements are smooth and flat skeletal elements, much thinner and smaller than the surrounding supracentrals. The excellent preservation of the material of *”P.” melchiori* in very fine-grained siltstones suggests that the absence of pustulipores is likely genuine, and not the result of a taphonomic bias (Figs. 6A-E, 7).

The reexamination of the holotype and several new, better-preserved specimens of *”Bohemiaecystis” zagoraensis* (upper part of the Fezouata Formation, Floian; Anti-Atlas, Morocco) did not confirm the presence of a lamellate organ in this taxon, but did reveal the occurrence of more than 25 closely packed pairs of opposite U-shaped plates surrounding slit-like cothurnopores covered with minute smooth platelets, with no evidence of cone-shaped structures (Fig. 6F-H). Less-well preserved proto-lamellate organs are also present in undescribed scotiaecystids from the lower Tremadocian Pupusa Formation of the Jujuy Province (Argentina) and the lower part of the Fezouata Formation (late Tremadocian) of the Anti-Atlas, Morocco (see Lefebvre et al., 2016, 2019; Saleh et al., 2023). However, disjunct cothurnopores are not restricted to scotiaecystids, but are also present in other cornutes (Table 1), such as *Flabellicarpus rushtoni* from the Shineton Shale Formation (late Tremadocian) of Shropshire, UK (Martí Mus, 2002), the yet undescribed ”Tizagzaouine cornute” from the lower part of the Fezouata Formation (late Tremadocian) of the Anti-Atlas, Morocco (Martin et al., 2015; Lefebvre et al., 2022), and possibly, in the poorly-known cornute from the Whipple Cave Formation (Cambrian Stage 10) of Nevada, USA, tentatively identified as *Scotiaecystis?* sp. by Sumrall et al. (1997).

In summary, reexamination of the accessory orifices of *”P.” melchiori* confirms their identification as cothurnopores (Ubaghs, 1983, 1994), i.e. elliptical orifices surrounded by opposite U-shaped plates. However, in *Proscotiaecystis* and several other cornutes (e.g. *”B.” zagoraensis*, *F. rushtoni*), the pairs of U-shaped plates are particularly numerous and are laterally sutured to one another, forming an elongate proto-lamellate organ. The conjunct cothurnopores are slit-like, covered by a thin layer of polyplated integument, apparently without any evidence of pustulipores.

Lamellate organs

Lamellate organs are elongate, fusiform to crescent-shaped structures found exclusively in a small clade of derived scotiaecystids comprising the three genera *Bohemiaecystis*, *Scotiaecystis*, and *Thoralicarpus* (Fig. 8) (Lefebvre et al., 2022). Their outline, extension and location on the right anterior corner of the theca correspond relatively closely to those of accessory orifices in other cornutes (see above). In both external and internal aspects, lamellate organs appear as consisting of numerous, elongate ridges or ”lamellae” separated by narrow, slit-like grooves (Fig. 3).

The lamellae are all roughly perpendicular to the right margin of the theca. Within a same lamellate organ, the width of the lamellae remains the same (it is usually comprised between 0.15 and 0.22 mm), while their length regularly decreases towards both anterior and posterior ends of the organ. The number of lamellae increases with growth, with new elements being regularly added at the two extremities of the lamellate organ. For example, in *Thoralicarpus bounemrouensis* (Izegguirene Formation, early Sandbian; Anti-Atlas, Morocco), the number of lamellae increases from about 25 in the smallest and youngest individuals to over 60 in the largest, putatively older ones (Lefebvre et al., 2022). In all observed specimens of other scotiaecystid taxa with lamellate organs (i.e. *B. bouceki*, *B. chouberti*, *B. griffei*, *S. collapsa*, *S. curvata*, *T. guilloui*, *T. jefferiesi*, *T. prokopi*), the number of lamellae is also between 25 and 45.

In external view (Fig. 3A), all lamellae display a faint transverse suture, dividing them into two subequal (e.g. *Bohemiaecystis griffei*) or unequal parts (e.g. *Scotiaecystis collapsa*, *Thoralicarpus bounemrouensis*) (Fig. 8) (see also Bather, 1913; Jefferies, 1968; Ubaghs, 1968b, 1969; Cripps, 1988; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). Detailed observation of the lamellate organs also confirms the presence of a faint longitudinal suture dividing all lamellae into two subequal halves along most of their length (see Bather, 1913; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). This faint longitudinal suture is particularly visible when the lamellae are slightly weathered (Fig. 8A, B). However, in external view, this faint suture does not reach the rounded admarginal and abmarginal ends of the lamellae (Figs. 3A, 8A, B).

These observations imply that each lamella actually corresponds to two opposite, laterally compressed U-shaped plates (see Bather, 1913). The transverse line represents the suture between the two skeletal elements, while the faint longitudinal line corresponds to the contact between lateral branches of the U-shaped plates (Fig. 3A). Therefore, the main difference between a proto-lamellate and a lamellate organ is that the cothurnopores are still present, although narrow and elongate in the former, while they are closed in the latter. In *Scotiaecystis curvata* (Threave Glen Formation, late Katian; Scotland, UK), Bather (1913) reported the presence of minute platelets covering the longitudinal suture of lamellae (i.e. above the closed conjunct cothurnopores). Although such plates exist in cornutes with a proto-lamellate organ (see above), no evidence confirming their presence could be observed in *S. curvata*, as well as in other scotiaecystids with a lamellate organ. It is therefore likely that Bather (1913) was misled by the preservation of *S. curvata* in a relatively coarse-grained lithology (Ubaghs, 1968b, 1969).

In *Bohemiaecystis* and *Thoralicarpus*, lamellate organs are particularly high, rising above the supracentral area and penetrating deep into the thecal cavity (Fig. 8A-D, F-G). The height of the lamellae is greatest along the suture between the anterior and posterior U-shaped elements. In most of these taxa, the anterior (admarginal) part of the lamella is more shallowly inclined than the

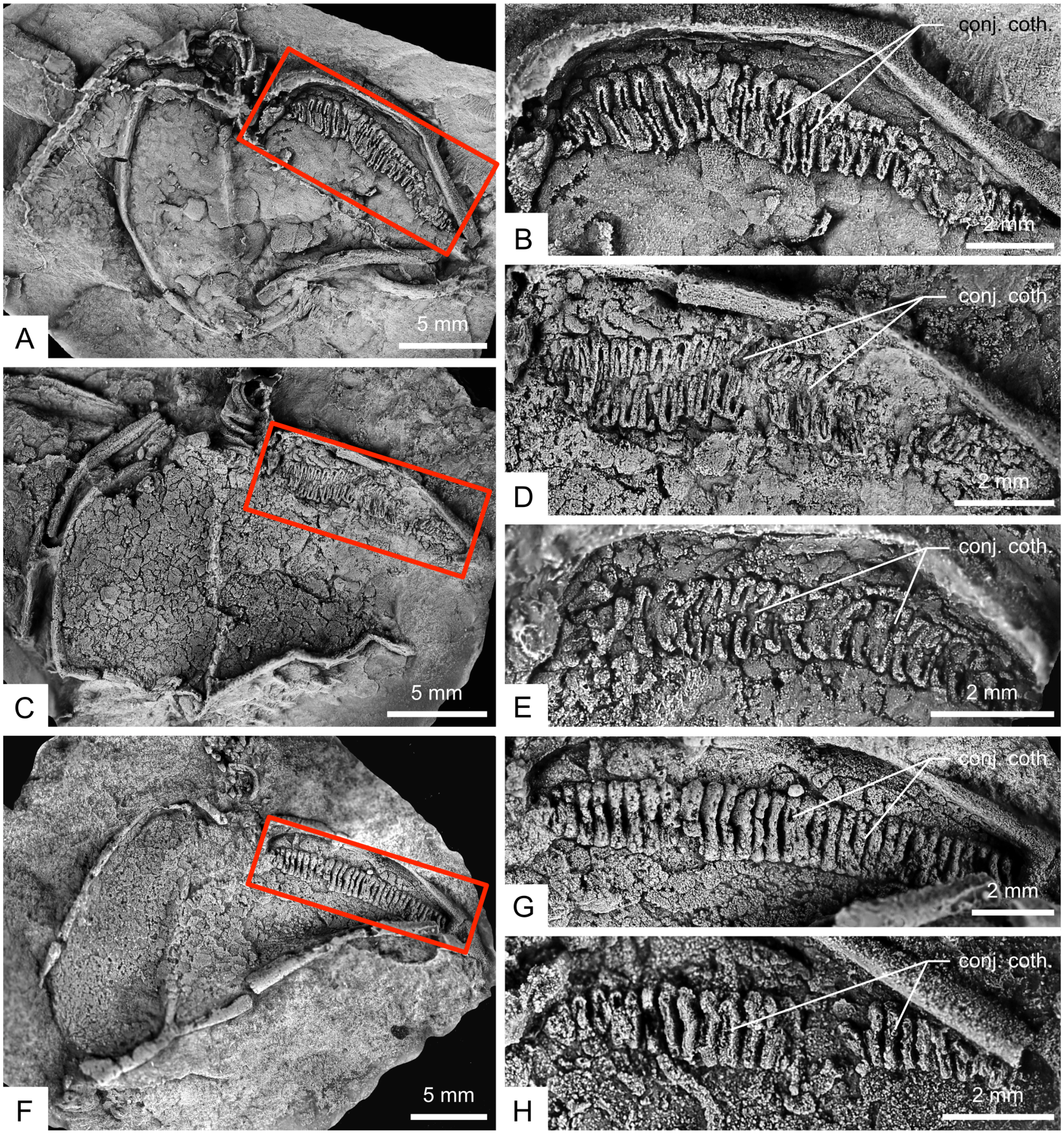

Figure 6. Respiratory structures in cornutes: proto-lamellate organs; latex casts of original specimens. (**A–E**) *Thoralicystis melchiori*, Landeyran Formation (Floian, Lower Ordovician), Montagne Noire, France; all specimens in upper aspect. (**A–B**) UCBL-FSL.712807, holotype. (**A**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (B). (**B**) Proto-lamellate organ in the right anterior corner of the supracentral area. (**C–D**) UCBL-FSL712810. (**C**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (D). (**D**) Proto-lamellate organ in the right anterior corner of the upper thecal surface. (**E**) UCBL-FSL712809; proto-lamellate organ in the right anterior corner of the supracentral area. (**F–H**) *Thoralicystis zagoraensis*, upper part of the Fezouata Formation (Floian, Lower Ordovician), central Anti-Atlas, Morocco; all specimens in upper aspect. (**F–G**) IGR.16687, holotype. (**F**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (G). (**G**) Proto-lamellate organ in the right anterior corner of the supracentral area. (**H**) UCBL-FSL.711599. Proto-lamellate organ in the right anterior corner of the upper thecal surface. Abbreviation: conj. coth., conjunct cothurnopores.

posterior (abmarginal) one (Fig. 8A-D, F-G). In *Scotiaecystis*, the lamellate organs are much lower, appearing as almost flat structures. In *S. curvata* (Figs 3, 8E), the lamellae are slightly convex and chevron-shaped (externally), while they are almost flat to slightly concave in *S. collapsa* (Bather, 1913; Jefferies, 1968; Cripps, 1988; Lefebvre et al., 2022).

In both external and internal aspects, the width of the narrow, elongate inter-lamellar slits remains approximately the same and ranges between 0.07 and 0.15 mm (see also Ubaghs, 1969; Lefebvre et al., 2022). However, detailed observation of the lamellate organs of scotiaecystids confirms that lamellae are not separated by actual slits (i.e. body openings; see Ubaghs, 1968b, 1969; Lefebvre and Vizcaïno, 1999; Smith, 2005; Lefebvre et al.,

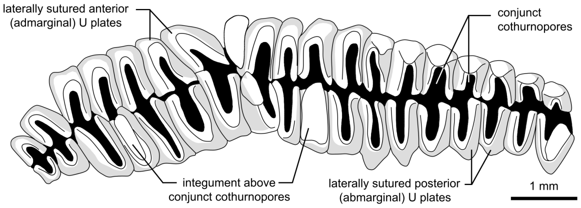

Figure 7. Camera-lucida drawing of the proto-lamellate organ of the holotype of *Thoralicystis melchiori* (UCBL-FSL.712807), Landeyran Formation (Floian, Lower Ordovician), Montagne Noire, France, with integumentary platelets preserved above some of its numerous, narrow, elongate and tightly sutured conjunct cothurnopores.

2022), but by deep furrows excavated between the vertical walls of neighbouring, tightly sutured lamellae (see e.g. Jefferies, 1968). The internal view of lamellate organs is particularly misleading (Fig. 3B), as it presents a regular series of ridges separated by deep furrows, superficially similar to the lamellae and grooves visible in external aspect (Fig. 3A). However, internal grooves correspond to the narrow, elongate external ridges (lamellae), while the internal ridges are equivalent to the external grooves. This identification is confirmed by the presence of clear U-shaped structures at both ends of each internal groove (see Jefferies, 1968), and by the observation that each internal ridge splits anteriorly (admarginally) and posteriorly (abmarginally) into two lateral branches (see Bather, 1913).

In summary, lamellate organs do not consist of a series of narrow slit-like openings separated by lamellae (see Ubaghs, 1968b, 1969; Parsley, 1988; Lefebvre and Vizcaïno, 1999; Smith, 2005; Lefebvre et al., 2022). Rather, lamellate organs correspond to strongly folded thecal structures resulting from the adjoining of numerous hollow, sutured lamellae, separated from each other by more or less deep grooves (see e.g. Jefferies, 1968; Cripps 1988). Furthermore, lamellate organs show no evidence of putative articulation between adjacent lamellae (see e.g. Jefferies, 1968, 1986; Smith, 2005). On the contrary, neighbouring lamellae are tightly sutured to each other, preventing any movement and/or rupture of the lamellate organ, which formed a fragile but rigid structure. New observations do not confirm that the lamellae are composite structures resulting from the suture between the lateral branches of two neighbouring pairs of U-shaped plates (see e.g. Jefferies, 1968; Cripps, 1988; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). Rather, each lamella corresponds to a pair of opposite, strongly laterally compressed U-shaped plates, homologous to those occurring in conjunct cothurnopores (see Bather, 1913).

Discussion

Sutural pores are the plesiomorphic condition in cornutes

The orifices present over a large part of the supracentral area of *Nevadaecystis* (Fig. 1C), as well as those restricted to the right anterior corner of this surface in *Ceratocystis* (Figs. 1A, B, 4A) are morphologically identical to the sutural pores present in many other Cambrian echinoderms. The delicate stellate supracentrals of *Nevadaecystis* (Fig. 1C) resemble the thecal plates of several eocrinoids (e.g. *Akadocrinus jani*, *Globoeocrinus globulus*, *Gogia palmeri*, *Sineocrinus lui*; see e.g. Sprinkle, 1973; Parsley and Zhao, 2006; Zhao et al., 2008; Nohejlová and Fatka, 2016). This stellate morphology is typical of thin thecal plates bearing numerous sutural pores along their contacts with surrounding skeletal elements. It is therefore reasonable to consider that the sutural pores shared by the large stellate supracentrals of *Nevadaecystis* were housing exothecal respiratory structures (epispires) homologous to those present in many other Cambrian echinoderms (Ubaghs, 1968b; Lefebvre and Vizcaïno, 1999; Smith, 2005; Lefebvre et al., 2022).

In *Ceratocystis* (Figs. 1A, B, 4A), the morphology of sutural pores is similar, but their distribution is more limited, and they are present across the sutures between thicker thecal plates. In many basal blastozoans (e.g. *Akadocrinus jani*, *Gogia* sp., *Sinoeocrinus lui*), the location of sutural pores is often restricted to the adoral (apical) part of the theca, at least in juvenile stages (Parsley, 2012; Zamora et al., 2013; Nohejlová and Fatka, 2016). The same situation occurs in *Ceratocystis*, where sutural pores are restricted to the adoral part of the theca (i.e. next to the aulacophore insertion, and thus, the mouth), and more precisely, to the right part of the supracentral area, next to the hydropore (Ubaghs, 1967, 1968b; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). As pointed out by Smith (2005), the sutural pores of *Ceratocystis* do not show any evidence supporting their interpretation as outlet valves.

Considering them as branchial openings (e.g. Jefferies, 1969, 1986) is therefore totally *ad hoc*, and based solely on the interpretation of cothurnopores in younger and more derived cornutes. Instead, the thecal orifices of *Ceratocystis*, which are morphologically identical to the sutural pores of thick-plated eocrinoids (e.g. *Gogia gondi*, *Lichenoides priscus*, *Rhopalocystis destombesi*; see Ubaghs, 1953, 1963, 1968a, 1987) probably housed similar exothecal respiratory structures (i.e. epispires). The presence of platelets covering the sutural pores of *Ceratocystis* suggested by Jefferies (1969) could not be confirmed, but it cannot be completely excluded, as such ”cover plates” have been documented in some eocrinoids (e.g. *Alanisicystis andalusiae*, *Gogia parsleyi*, *Rhopalocystis destombesi*; Ubaghs, 1963, 1968a; Sprinkle, 1973; Ubaghs and Vizcaïno, 1990; Zamora et al., 2009).

Disjunct cothurnopores are modified sutural pores

Like the sutural pores of *Ceratocystis*, *Nevadaecystis* and many other Cambro-Ordovician echinoderms (see above), disjunct cothurnopores are rounded to elliptical orifices always located across the suture between two skeletal elements. They can therefore be reasonably interpreted as a highly modified type of sutural pores (Parsley, 1988; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022). This interpretation also seems to be supported by the U-shaped morphology of each of the two plates sharing a cothurnopore (Fig. 2): similar U-shaped ridges are generally present around sutural pores in eocrinoids (e.g. *Akadocrinus jani*, *Globoeocrinus globulus*, *Lichenoides priscus*, *Sinoeocrinus lui*; Ubaghs, 1953, 1968a; Sprinkle, 1973; Parsley and Zhao, 2006; Zhao et al., 2008; Nohejlová and Fatka, 2016; Sheffield et al., 2022).

The main difference between cothurnopores and classical sutural pores is that, in the latter, each thecal plate may have several orifices, while in cothurnopore-bearing taxa, a specific pair of skeletal elements is closely associated to each pore. In cornutes, this arrangement possibly results from the transition from thick-plated supracentral areas with classical sutural pores (plesiomorphic condition: *Ceratocystis*) to extensive, thinly plated, and probably flexible integumentary surfaces in more derived taxa. In all cothurnopore-bearing cornutes, the restricted distribution of these orifices in the right anterior corner of the upper thecal surface further supports the idea that they probably derive from the similarly located

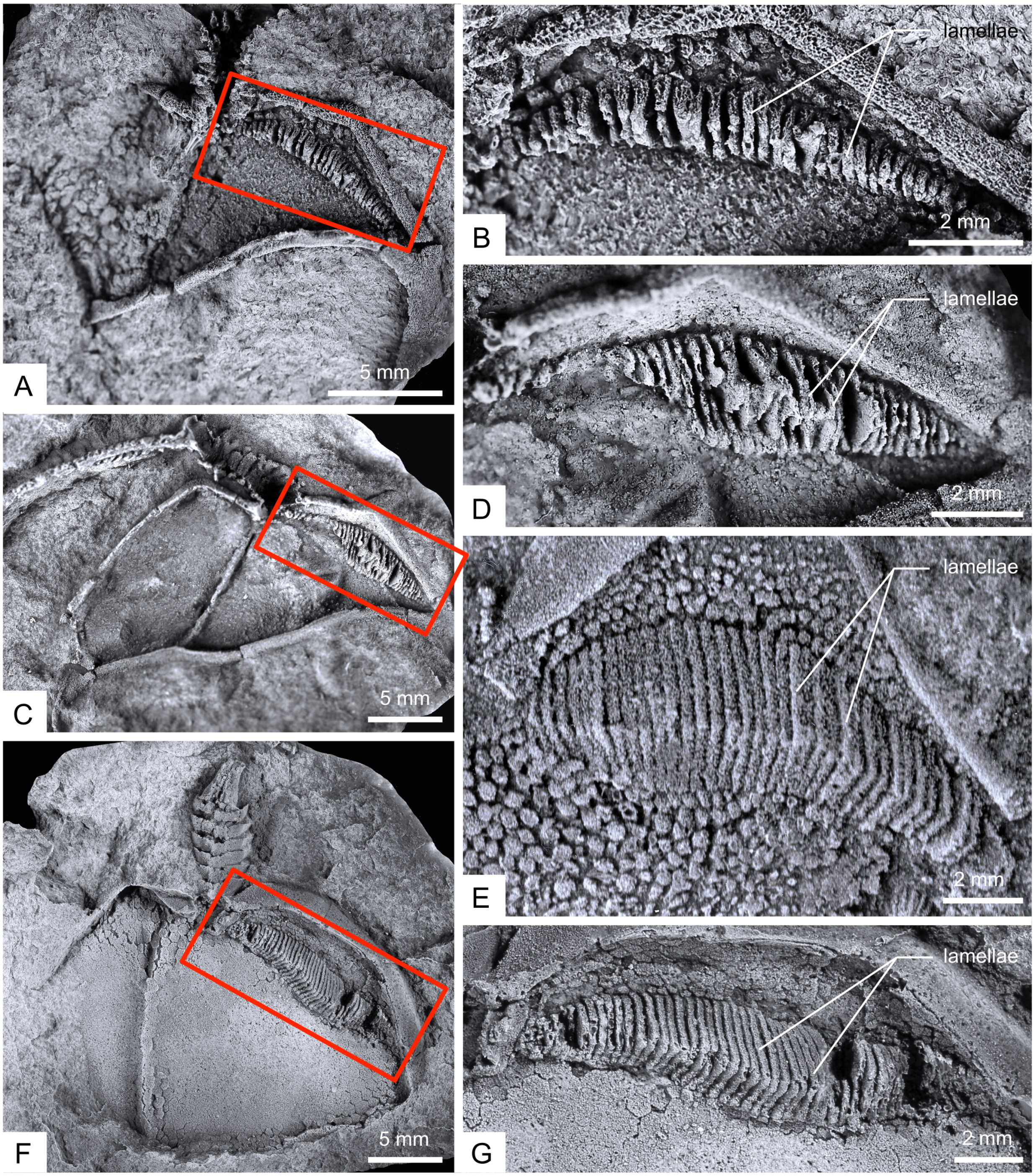

Figure 8. Respiratory structures in cornutes: lamellate organs; latex casts of original specimens. (**A–D**) *Bohemiaecystis griffei*, Saint-Chinian Formation (Tremadocian, Lower Ordovician), Montagne Noire, France; all specimens in upper aspect. (**A–B**) UCBL-FSL.713152. (**A**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (B). (**B**) Lamellate organ in the right anterior corner of the upper thecal surface. (**C–D**) UCBL-FSL.711699. (**C**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (D). (**D**) Lamellate organ in the right anterior corner of the supracentral area. (**E**) *Scotiaecystis curvata*, BMNHUK.E.23129, holotype, Threave Glen Formation (Katian, Ordovician), Scotland, UK. Lamellate organ in the right anterior corner of the upper thecal surface. (**F–G**) *Bohemiaecystis bouceki*, NMP.L.17728, holotype, Dobrotivá Formation (Darriwilian, Middle Ordovician), Prague Basin, Czech Republic. (**F**) Upper thecal surface and part of the aulacophore; the red box indicates the location of (G). (**G**) Lamellate organ in the right anterior corner of the supracentral area.

sutural pores of *Ceratocystis* (Bather, 1913; 1926; Gislén, 1930; Ubaghs, 1967; Jefferies, 1969; Parsley, 1988; Cripps, 1991; Smith, 2005; Lefebvre et al., 2022).

Within each elliptical structure formed by a pair of opposite U-shaped plates, the presence of numerous minute skeletal elements completely covering the disjunct cothurnopore is confirmed (Fig. 2C) (Bather, 1913, 1926, 1930; Ubaghs, 1963, 1968b, 1969; Jefferies, 1968, 1986; Woods and Jefferies, 1992; Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022; Jackson, 2024). However, these platelets do not display the alternating (zigzag) biserial pattern typical of ambulacral cover plates suggested by Bather (1913, 1926, 1930) (Fig. 2A), nor do they form a rigid, mobile flap articulated to the posterior U-plate (Fig. 2B), as assumed by Jefferies (1968, 1969, 1986; see also e.g. Woods and Jefferies, 1992; Smith, 2005). Instead, these minute skeletal elements form one or two rows of small truncated cones, each bearing a tiny apical orifice (Figs. 2C, 9A) (Ubaghs, 1969; Lefebvre and Vizcaïno, 1999; Jackson, 2024). The existence of small pustulipores enclosed in the elliptical structures of the cornutes, originally observed in some well-preserved specimens of *Phyllocystis blayaci* (Ubaghs, 1969; Lefebvre and Vizcaïno, 1999) has also been highlighted in a cornute indet. from Korea (Lee et al., 2005) and, based on high-resolution 3D CT-scan reconstructions, in *Cothurnocystis elizae* (Jackson, 2024).

These observations demonstrate that disjunct cothurnopores were neither multiple mouths associated with ambulacral cover plates, nor gill openings with a mobile flap, but highly specialized covered sutural pores more closely resembling those found in some eocrinoids (e.g. *Alanisicystis andalusiae*, *Rhopalocystis destombesi*; see Ubaghs, 1963, 1968a; Sprinkle, 1973; Ubaghs and Vizcaïno, 1990; Sheffield et al., 2022). However, while the thecal respiratory orifices are protected by a simple layer of thin plates in *Alanisicystis* and *Rhopalocystis*, they are covered by a more complex arrangement of skeletal elements forming numerous small perforated cones in cornutes (Figs. 2C, 9A). Disjunct cothurnopores therefore most likely represent exothecal respiratory structures, probably analogous to the covered epispires of eocrinoids, and derived from classical sutural pores comparable to those present in *Ceratocystis* and many other Cambrian echinoderms (Lefebvre and Vizcaïno, 1999; Lefebvre et al., 2022; Jackson, 2024).

Phyllocystis crassimarginata: the only cornute with large pustulipores

The possession of large pustulipores is an autapomorphy of *Phyllocystis crassimarginata* (Figs. 4B, 5E-G) (see Ubaghs, 1968b, 1969; Lefebvre and Vizcaïno, 1999). The presence of disjunct cothurnopores, with minute pustulipores enclosed in U-shaped plates, in the closely related taxon *P. blayaci* (Figs. 2C, 4C, D) calls into question the possibility that the acquisition of larger pustulipores in *P. crassimarginata* may have resulted from the loss of the U-shaped plates. This interpretation is in good agreement with the similar extension of isolated pustulipores (in *P. crassimarginata*) and disjunct cothurnopores (in *P. blayaci*) in the right anterior corner of the supracentral area, but also with the secondary alignment of pustulipores, mimicking the arrangement of cothurnopores, in large individuals of *P. crassimargata* (Fig. 5F, G).

Reexamination of pustulipores (both the minute ones associated with disjunct cothurnopores and the larger ones of *P. crassimarginata*) provided no evidence of articulation and/or putative closing device(s), which would support their interpretation as outlet valves (Smith, 2005), but rather confirmed that they consist of rounded to elliptical wide-open orifices surrounded by a thickened lip and located atop a small cone made of two or more plates (Ubaghs, 1968b, 1969; Lefebvre and Vizcaïno, 1999). By analogy with similar body openings present in many early Palaeozoic echinoderms (e.g. sutural pores, diplopores) and extant asteroids, it is therefore very likely that pustulipores were housing soft, papulae-like exothecal respiratory structures.

Nevadaecystis: the only cornute with two types of respiratory structures

Nevadaecystis is the only cornute with two different types of thecal orifices (sutural pores and disjunct cothurnopores) on its upper thecal surface (Fig. 1C). Since sutural pores are universally considered to be respiratory structures, many authors have questioned the possibility that cothurnopores could have fulfilled the same function, considering it unlikely that two different types of respiratory structures could be present in the same organism (Ubaghs, 1963, 1968b; Smith, 2005). However, extant echinoderms present numerous examples showing that the same organism can respire by several means (Shick, 1983; Brusca et al., 2016). Moreover, the combination of two different types of respiratory structures in a single taxon is not unique to *Nevadaecystis*, but has been also documented in the blastoid *Troosticrinus*, which exhibits coronal canals and hydrospires (Sumrall and Waters, 2012; Sheffield et al., 2022).

Transition from disjunct to conjunct cothurnopores

The proto-lamellate organ of "*Proscotiaecystis*" *melchiori* (Figs. 6A-E, 7) consists of numerous narrow conjunct cothurnopores enclosed by elongate, packed, and tightly sutured pairs of U-shaped plates (Ubaghs, 1983, 1994). However, contrary to the situation in cornutes with fewer, larger, and isolated disjunct cothurnopores, the slit-like conjunct cothurnopores of proto-lamellate organs are apparently not covered by numerous small pustulipores, but by a narrow strip of minute, thin and smooth platelets (Figs. 5B, D, E, G, H, 7). In *"P." melchiori* and other cornutes with a proto-lamellate organ, each slit-like conjunct cothurnopore therefore opens into a totally closed, elongate, fully calcified, external lamella formed by the two low U-shaped plates surrounding it, and the overlying narrow strip of integument (Fig. 9B). This implies that the proto-lamellate organs of *"P." melchiori* and allied forms are entirely calcified exothecal respiratory structures, and therefore, more or less analogous to the covered epispires of some eocrinoids (e.g. *Alanisicystis*, *Rhopalocystis*; Ubaghs, 1963, 1968a; Sprinkle, 1973; Ubaghs and Vizcaïno, 1990; Sheffield et al., 2022) and/or the humatirhombs of caryocystitoid rhombiferans (e.g. *Lophotocystis*, *Ulrichocystis*; Paul, 1972; Sheffield et al., 2022).

Transition from conjunct cothurnopores to lamellipores

In more derived scotiaecystids (*Bohemiaecystis*, *Thoralicarpus*, *Scotiaecystis*), the two branches of each U-shaped plate are sutured to each other along their upper margins (Figs 3, 9C). The lamellae of lamellate organs are therefore equivalent to the external folds of proto-lamellate organs and also to the pairs of opposite U-shaped elements of disjunct cothurnopores (Bather, 1913). While small orifices (pustulipores) probably housing papulae-like soft vesicles are present in disjunct cothurnopores, both the proto-lamellate and lamellate organs represent totally closed folded structures. Their presumed respiratory function is supported by the highly porous microstructure of their thin and delicate lateral walls (Parsley, 1988; Lefebvre and Vizcaïno, 1999), as well as by their overall morphology, remarkably convergent with the pectinirhombs of glyptocystitoid rhombiferans (Bather, 1913; Ubaghs, 1968b; Parsley, 1988; Lefebvre and Vizcaïno, 1999; Smith, 2005; Jackson, 2024).

This analogy particularly makes sense in the case of the lamellate organs of *Bohemiaecystis* and *Thoralicarpus*, both characterized by high lamellae, forming deep folds of the thecal wall. From a functional point of view, the lamellate organ of *Scotiaecystis* (with

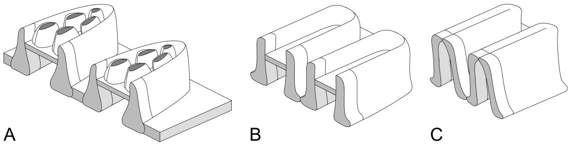

Figure 9. Schematic reconstructions of respiratory structures in cornutes, to illustrate the transition from disjunct cothurnopores (**A**) to conjunct cothurnopores (proto-lamellate organ) (**B**), and lamellate organs (**C**).

low lamellae) is more comparable to the humatirhombs of caryocystitoid rhombiferans. Technically, cothurnopores are still present in lamellate organs: they correspond to the narrow internal grooves located inside each lamella (Fig. 3B). The term ”lamellipores” originally proposed for slit-like orifices by Ubaghs (1968b) is retained here, to designate the narrow, elongate intrathecal orifices located at the base of lamellae (i.e. laterally compressed and externally closed U-shaped plates) (Table 1). Disjunct cothurnopores (Fig. 9A), proto-lamellate organs (Fig. 9B) and lamellate organs (Fig. 9C) therefore represent different morphotypes belonging to a single and broad morphological spectrum of respiratory structures derived from classical sutural pores.

Implications for the systematics of scotiaecystid cornutes

In their revision of scotiaecystid systematics, Lefebvre et al. (2022) identified four main morphotypes based on the morphology of their respiratory structures and the number of posterior thecal spines. They suggested assigning to *Proscotiaecystis* all scotiaecystids bearing two posterior spines (digital and glossal), and a proto-lamellate organ; to *Bohemiaecystis*, all taxa with two spines, and a lamellate organ composed of high lamellae; to *Thoralicarpus*, forms with a single spine (the digital spine being lost), and a lamellate organ also consisting of high lamellae; and to *Scotiaecystis*, those with a single spine and a lamellate organ made up of low lamellae. Based on the original description of *Thoralicystis zagoraensis* by Chauvel (1966), and the putative presence of two posterior spines and a lamellate organ in this cornute, Lefebvre et al. (2022) considered *Thoralicystis* Chauvel, 1971 as a junior synonym of *Bohemiaecystis* Caster in Ubaghs, 1968b. This conclusion is, however, not confirmed by the re-examination of the type material of this taxon (Fig. 6F, G), and the observation of numerous, better preserved specimens (Fig. 6H), all showing the presence of a proto-lamellate organ consisting of numerous, closely packed cothurnopores. This implies that *Thoralicystis zagoraensis* and *Proscotiaecystis melchiori* share the same organization (i.e. two posterior spines and a proto-lamellate organ) and belong to the same genus. Therefore, *Proscotiaecystis* Ubaghs, 1994 is considered a junior synonym of the genus *Thoralicystis* Chauvel, 1971, which is hereby reinstated as valid.

Conclusions

Detailed morphological analysis of ”accessory structures” present on the upper thecal surface of cornutes does not support their interpretation as multiple mouths (no evidence of ambulacral cover plates), gonopores, or gill openings (they are not constructed as outlet valves, and there is no evidence of any flap).

Plesiomorphically (in basal cornutes), they consist of sutural pores, morphologically identical to those present in many other Cambrian echinoderms. In some more derived taxa, the cothurnopores, either disjunct (isolated) or conjunct (grouped in a proto-lamellate organ) correspond to highly specialized covered sutural pores, each delimited by a pair of U-shaped skeletal elements. In lamellate organs, the lamellipores correspond to totally closed cothurnopores, whose associated U-shaped plates, strongly compressed, form numerous folds separated by more or less deep furrows. In most taxa, the limited distribution of respiratory structures in the same crescent-shaped area located in the right anterior thecal corner suggests interaction with underlying, probably folded, soft parts involved in gas exchanges.

Like the diplopores of ”cystoids” (see e.g. Paul and Toom, 2021), cornute respiratory structures thus originated from sutural pores, which represent the plesiomorphic condition at the phylum scale (see e.g. Mooi et al., 2024). This implies that disjunct cothurnopores, pustulipores, proto-lamellate and lamellate organs, derived from standard echinoderm respiratory structures, are not homologous to the gill slits of other deuterostomes.

Data availability

All examined specimens are housed in public collections and accessible upon request.

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Author contributions

All co-authors contributed to the original draft and revision of the MS and casting of the specimens. Drawings were made by CD and BL, measurements and data analysis by MM, and photographs by EB.

Competing interests

The authors declare no conflicts of interests.

Ethics and AI use

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