



Gigantism, taphonomy and palaeoecology of *Basiloceras*, a new oncocerid genus from the Middle Devonian of the Tafilalt (Morocco)

Alexander Pohle¹ · Christian Klug¹ · Mischa Haas^{2,3}

Received: 13 September 2018 / Accepted: 16 January 2019 / Published online: 31 January 2019
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Abstract

The genus *Basiloceras* gen. nov. containing the two species *B. goliath* sp. nov. and *B. david* sp. nov. is described. It belongs to the Acleistoceratidae within the Oncocerida. Both species are from the Middle Devonian of the Tafilalt (Morocco). The genus exhibits a large interspecific size range between the small Eifelian *B. david* sp. nov. and the Givetian *B. goliath* sp. nov., the largest Devonian oncocerid currently known, altogether only second to some fragmentary remains of *Calchasicerias* from the Carboniferous of Russia. Several other large species are mainly known from the late Emsian of Bohemia and the Eifelian of Germany. The holotype of *B. goliath* sp. nov. contains numerous epicoles, trace fossils and shell debris, which are discussed in the context of its taphonomy. Compared to other oncocerids, *Basiloceras* is characterised by a short body chamber, which might be related to buoyancy regulation. In contrast to some older publications, we do not regard breviconic oncocerids with contracted aperture as benthic or nektobenthic animals, but instead, we think that they dwelled in the water column.

Keywords Oncocerida · Cephalopoda · Gigantism · Epicoles · Taphonomy · Buoyancy

Introduction

Devonian non-ammonoid cephalopods from the Tafilalt of Morocco have long been treated only cursorily by researchers, despite the intense palaeontological research that has been carried out in the region for almost a century (for a literature review, see Becker et al. 2018; Klug and Pohle 2018 and references therein). After the pioneering work of Termier and Termier (1950), which included several descriptions of nautiloids amongst many other fossil groups, no significant contributions were made for about 50 years, until increased scientific effort resulted in several studies that included nautiloids in the past decade

(Kröger et al. 2005; Klug 2007; Klug et al. 2008; Kröger 2008; De Baets et al. 2010; Frey et al. 2014; De Baets and Munneke 2018; Pohle and Klug 2018a, b). Nevertheless, many specimens await proper taxonomic descriptions as new material is still being recovered.

Here, we describe an unusually large oncocerid that was collected near Rich Tamirant between El Khraouia and Oum El Hadej in the southern Tafilalt (Morocco) from Givetian rocks (Fig. 1). We introduce the new genus *Basiloceras*, which includes the two species *Basiloceras goliath* sp. nov. from the Givetian and *B. david* sp. nov. from the Eifelian. We also discuss the systematic position of the genus and the taphonomy of the type species.

Editorial Handling: D. Marty.

✉ Alexander Pohle
alexander.pohle@pim.uzh.ch

¹ Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid-Strasse 4, 8006 Zurich, Switzerland

² Department of Earth Sciences, ETH Zürich, Sonneggstrasse 5, 8006 Zurich, Switzerland

³ Department of Surface Waters Research and Management, Eawag, Überlandstrasse 133, 8600 Dübendorf, Switzerland

Materials and methods

We mostly use the terminology of the Treatise (Sweet 1964; Teichert 1964) with the addition of the term actinosiphonate lamellae in preference to actinosiphonate deposits to more clearly distinguish them from the endosiphuncular deposits of the Orthocerida or Actinocerida (see also Flower 1943, 1964; Crick and Teichert 1979; Mutvei 2011). Also note that height always refers to

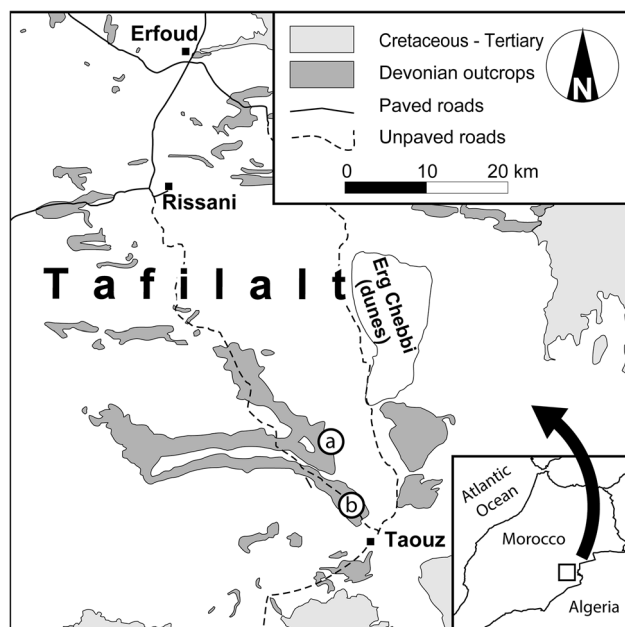


Fig. 1 Geological map of the southern Tafilalt. **a** Type locality of *Basiloceras goliath*, near Rich Tamirant. **b** Type locality of *B. david*, the Jebel Ouafoufal

measurements in dorsoventral direction, width to measurements in lateral direction and length to measurements in longitudinal direction of the conch. Furthermore, a contracted body chamber has its smallest diameter at the peristome, while a constricted aperture has its smallest diameter behind the peristome. We orient the specimens on figures with the aperture downwards, in accordance with Stridsberg (1985, 1990a) and Pohle and Klug (2018b).

All specimens are housed at the Paläontologisches Institut und Museum of the Universität Zürich, Switzerland (PIMUZ).

Previous reports of large Devonian oncocerids

Large species, sometimes dubbed giants (gigantism), evolved independently and numerous times in several clades of cephalopods (Landois 1895; Teichert and Kummel 1960; Stevens 1988; Manger et al. 1999; Kubodera and Mori 2005; Iba et al. 2015; Klug et al. 2015; Rosa et al. 2017; Pohle and Klug 2018a). However, in some groups such as the Oncocerida, giants are much less common (although this depends on the definition of giants; see Klug et al. 2015). In general, oncocerids are small, i.e. specimens with cross section diameters above 100 mm are rare; such taxa are accordingly here considered to be large. The species described here as *Basiloceras goliath* sp. nov. has a maximum conch width of at least 180 mm and is,

therefore, a true giant among the Oncocerida. To our knowledge, there is only one report of a possibly larger oncocerid: several specimens of *Calchasicerus ventricosus* (M'Coy, 1844) from the Early Carboniferous of Russia were reported by Shimansky (1968) to reach diameters between 180 and 240 mm.

Similar cases have been reported only occasionally from the Devonian. Most notably, Barrande (1865–1877) described and illustrated six very large species from the late Emsian of Bohemia: *Phragmoceras devonicans* Barrande, 1865, *Cyrtoceras empiricum* Barrande, 1877, *C. palinurus* Barrande, 1877, *C. lumbosum* Barrande, 1877, *C. turnus* Barrande, 1877 and *C. imperans* Barrande, 1877. Later, Foerste (1926) erected the genera *Paracleistoceras*, *Blakeoceras*, *Conostichoceras*, *Poteriocerina* and *Turnoceras* based on the former five of these species. All of these come from the late Emsian Třebotov limestone (there is some misunderstanding in the literature concerning the age of the Třebotov limestone; see Chlupáč et al. 1979; Chlupáč 1983; Manda and Turek 2011) and have a maximum diameter between 100 and 140 mm. The largest of Barrande's species, "*C. imperans*", reached diameters of 160 mm. However, as these remains are poorly preserved and the position of the siphuncle is unknown, the material of the latter species was not reinvestigated by later researchers. According to Dzik (1984), all the species mentioned above belong to the genus *Paracleistoceras*. Without having reinvestigated the original material, we tend to agree with Dzik's (1984) view, perhaps with the exception of the genus *Blakeoceras*, which differs from *Paracleistoceras* in its compressed cross section, stronger curvature and broader siphuncle.

Several other large species have been assigned to the genus *Cyrtoceratites* Goldfuss, 1830 (or many other, probably incorrect secondary spellings, such as *Cyrtoceras*, *Cyrtocera*, and *Cyrthoceratites*), however, most of them are markedly cyrtoconic or even gyroconic, and thus clearly differ from the less strongly curved Bohemian species and the straight *Basiloceras* gen. nov. One specimen from the Middle Devonian of Canada described as *Cyrthoceratites* aff. *C. lineatus* D'Archiac and De Verneuil, 1852 by Collins (1969) has a maximum conch diameter of 150 mm. More recently, another large "*Cyrtoceratites*" from the Eifelian of El Gara (Tafilalt) was reported by Afhüppe et al. (2018) and Becker et al. (2018).

It is apparent that the late Emsian to Eifelian was a period where several large oncocerid species occurred that share an exogastric conch curvature and a siphuncle with continuous actinosiphonate lamellae. However, as most of these species require revision, their taxonomic affinities are unclear. Various authors have placed them in the *Acleistoceratidae* Flower, in Flower and Kummel 1950, *Cyrtoceratidae* Chapman, 1857, *Jovellaniidae* Foord, 1888 or

Nothoceratidae Fischer, 1882 (Flower and Kummel 1950; Zhuravleva 1962, 1974; Sweet 1964; Dzik 1984). Curiously, no author placed all of them within the same family, despite the morphological similarities. Detailed studies of the siphuncular structures are needed to clarify whether gigantism occurred at the same time independently in several oncocerid lineages or whether these giants represent a monophyletic group. In contrast to the Bohemian and German giant oncocerids, the only known siphuncular segment of *Basiloceras* lacks actinosiphonate lamellae, which suggests that large size evolved independently at least twice in oncocerids during the Devonian. Possibly, the large size of these oncocerids evolved as a response to the rise of large arthrodiroids and chondrichthyans (Brett and Walker 2002; Klug et al. 2010, 2017; Dahl et al. 2011; Brazeau and Friedman 2015), which probably also preyed on cephalopods (Klug 2007).

Taphonomy

The holotype of *Basiloceras goliath* sp. nov. (PIMUZ 35928) shows some taphonomic peculiarities. After its death and the subsequent settling on the sediment surface, it came to rest on its dorsal side. This is corroborated by the sedimentary filling containing coarse bioclasts, by the better preservation of the dorsal side including peristome and phragmocone, and by the greater extent of phragmocone sediment filling. Remarkably, numerous fossils are associated with the cephalopod conch. Partially, the conch served as a benthic island (Seilacher 1982), as fossil trap and as cryptic habitat.

Encrustations of cephalopod shells by various organisms since the Ordovician have been reported in many publications (e.g., Watkins 1981; Baird et al. 1989; Davis et al. 1999; Klug and Korn 2001; Kröger et al. 2009; Landman et al. 2010; Rakociński 2011; Wyse Jackson and Key 2014; Hautmann et al. 2017). The surface of the holotype of *B. goliath* also shows remains of several epibionts and trace fossils, which allows us to make some inferences about its taphonomy (Fig. 2).

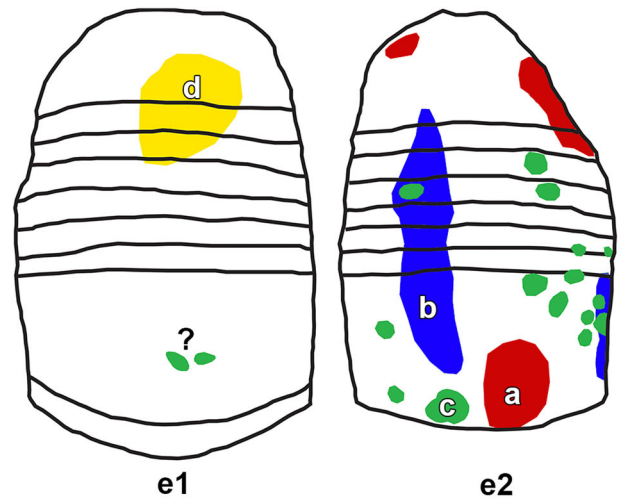
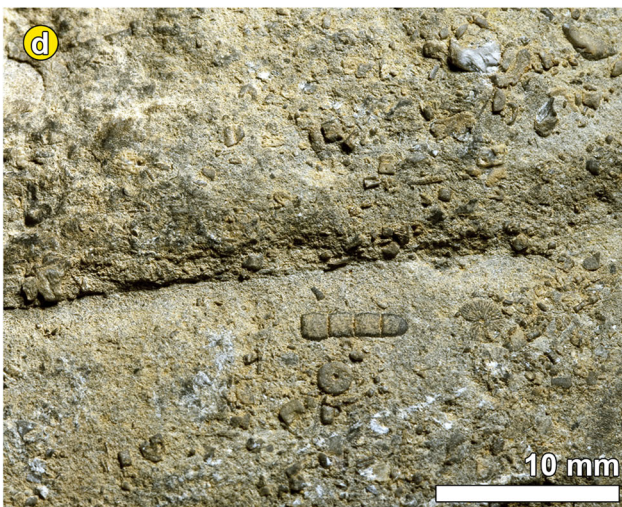
We recovered three articulate brachiopods from the inside of the dorsum of the incomplete phragmocone (Fig. 3). Although the preservation is poor, they clearly belong to different species, here provisionally assigned to cf. *Schizophoria* sp. (Fig. 3a, b), Gypidulidae indet. (Fig. 3c, d) and Orthida indet. (Fig. 3e) (personal communication Adam T. Halamski, July 2018). Finer taxonomic assignment is impossible, but there is some similarity to other Middle Devonian brachiopod associations from the eastern Anti-Atlas (compare, e.g., Halamski and Baliński 2013). These brachiopods were either settling on the conch, on the prefossilized specimen or washed into

the broken phragmocone by currents (fossil trap; cf. Wani 2007).

In addition, several valves of other brachiopods are visible at the surface of the body chamber and phragmocone (Fig. 2c). They are subcircular, appear to have a slightly thickened shell at the margin, concentric growth lines, and appear to be preserved in calcite. Some of them may belong to inarticulate brachiopods, which have been shown to frequently encrust Ordovician orthoconic nautiloids (Gabbott 1999) and Jurassic ammonites (Seilacher 1982), but many inarticulates have chitinophosphatic shells, which is not the case here. It is not even clear whether these valves are truly brachiopods or bivalves. The encrusters are almost entirely restricted to the ventral side (taphonomically the upper side) and only two very questionable specimens occur on the dorsum. They are not restricted to the body chamber and sometimes cross septa. Their appearance and preservation is reminiscent of the Triassic bivalve *Placunopsis*, which also often inhabited the inside of cephalopod conchs (e.g., Hölder 1990; Todd and Hagdorn 1993; Klug and Lehmkuhl 2004; Klug et al. 2004; Pruss et al. 2007).

Additionally, the ventral side of the conch carries about 30–40 corroded microconchids (Fig. 2b), small spiral tubes that were formed by organisms related to tentaculites (Weedon 1991; Taylor and Vinn 2006; Vinn 2006; Zatoń and Olempska 2017). Similar to the subcircular valves, they are only found on the ventral side of the conch of *B. goliath*. The microconchids may belong to the genus *Palaeoconchus* Vinn, 2006, one of only four genera known from the Devonian (Zatoń and Krawczyński 2011; Zatoń and Olempska 2017). However, this identification is provisional due to the poor preservation and the still very incomplete knowledge of this group. Currently, microconchids from Morocco have not received any attention, and thus they have not been investigated in systematic studies, although they have been reported to frequently encrust the Eifelian or Givetian brachiopod *Glyptogypa* (Halamski and Baliński 2013). Notably, we found no evidence of encrustation by crinoids, bryozoans, tabulate or rugose corals, which are also very common epicoles on cephalopod conchs (e.g., Klug and Korn 2001; Rakociński 2011; Wyse Jackson and Key 2014; Kröger and Aubrechtová 2018).

It is not entirely clear, whether the epicoles settled on the inside of the shell or on the internal mould. The microconchids are poorly preserved but judging from their appearance both interpretations appear possible (personal communication Olev Vinn, September 2018). The phragmocone is broken in one place, revealing that the septa were dissolved except for the outermost ridges; thus, the sutures are visible, but the septa did not provide obstacles for living or dead organisms to enter part of the



◀**Fig. 2** Post mortem epicoles of *Basiloceras goliath* sp. nov., holotype, PIMUZ 35927, Givetian, SE of Oum El Hadej. **a** (Red) trace fossils. **b** (Blue) microconchids, cf. *Palaeoconchus* sp. **c** (Green) encrusting bivalves or brachiopods. **d** (Yellow) shell debris, including shell fragments, small orthoconic cephalopods and crinoid columnals. **e** Outline of *B. goliath* sp. nov., holotype, PIMUZ 35927 in dorsal (e1) and ventral (e2) view. Colours indicate the distribution of trace fossils and epibionts on the conch

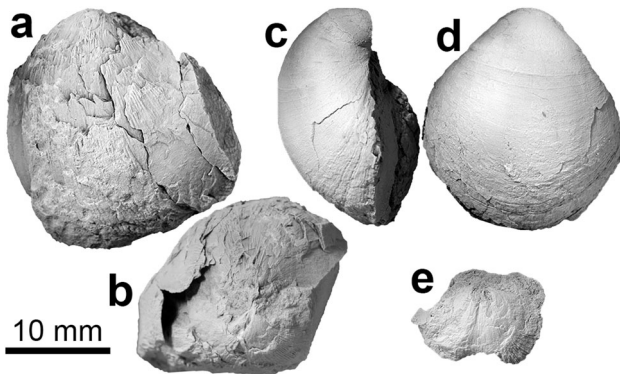


Fig. 3 Articulate brachiopods recovered from the phragmocone of *Basiloceras goliath* sp. nov., holotype, PIMUZ 35927, Givetian, SE of Oum El Hadej. All specimens were whitened with NH_4Cl . **a**, **b** Cf. *Schizophoria* sp., PIMUZ 35929, ventral and posterior view. **c**, **d** Gypidulidae indet., PIMUZ 35930, lateral and ventral view. **e** Orthida indet., PIMUZ 35931, ventral and lateral view

phragmocone. Alternatively, the septa were destroyed by another mechanism such as septal implosion during post-mortem descent (e.g., Westermann 1973, 1985; Stridsberg 1990b). However, we consider this as unlikely as the rich benthos associated with the specimen indicates that the depositional environment was probably too shallow to cause septal implosion. In any case, the microconchids and brachiopods possibly used the inside of the shell as a cryptic habitat, where they were protected from predators. The wealth of epibenthos and trace fossils associated with this oncocerid indicates that the conch was deposited in a well-oxygenated, moderately shallow water environment.

The dorsal side exposes large numbers of small shell fragments and crinoid columnals (Fig. 2d), but entirely lacks brachiopods, bivalves, microconchids or trace fossils, which corroborates that the specimen was deposited with the dorsal side facing downwards. The shell was partially broken and filled with sediment including numerous conchs and shell fragments of other organisms.

Ecological interpretation of *Basiloceras*

The body chamber of *Basiloceras* is short compared to other oncocerids. There are claims that the body chamber of oncocerids is usually large in comparison with the

phragmocone (e.g., Teichert 1967; Crick 1988; Frey 1989, 1995), however, a comparison with the literature suggests that both extremes exist and neither short nor long body chambers are significantly predominating (cf., e.g., Flower 1938; Sweet 1959, 1964; Zhuravleva 1972, 1974; Fyfe 1987). According to the mathematical hydrostatic models of Westermann (1975), body chamber length is inversely correlated to the apical angle of the shell, and thus brevicones would tend to have short body chambers. The large variation in body chamber size among oncocerids requires some further considerations concerning the significance of this character. Presumably, a short open body chamber offers less protection than a long contracted one but possibly allows for more flexibility and mobility in the soft parts. Furthermore, changes in body chamber proportions must have been accompanied or even controlled by adaptations of the buoyancy apparatus. According to Teichert (1967), a major feature of cephalopod evolution is the response to buoyancy problems, amongst which the relative size of the body chamber is one solution. As the soft body of the animal and particularly the shell itself have a higher density than sea water (e.g., Denton and Gilpin-Brown 1966; Lemanis et al. 2014; Tajika et al. 2015), the relative size of the body chamber had an important impact on the buoyancy of the animal (e.g., Teichert 1967; Crick 1988). A smaller body chamber would thus require further buoyancy regulating mechanisms such as an increased amount of cameral liquid to prevent the animal to float up to the sea surface. In the case of a vertical, aperture down orientation as in breviconic oncocerids, an increased amount of cameral liquid would have the additional effect of reducing the distance between the centres of buoyancy and mass, which would possibly enhance manoeuvrability and facilitate horizontal as well as vertical movement. A detailed analysis of oncocerid body chamber size and its hydrostatic implications is beyond the scope of this study, but there is a great potential for future studies. In particular, volume models of the conchs would help testing the buoyancy and reconstructing the amount of chamber water needed for neutral buoyancy (cf. Tajika et al. 2015; Naglik et al. 2016).

Although the material of *Basiloceras* does not directly provide new information on the buoyancy of breviconic oncocerids, we want to make a few general statements on their mode of life. Flower (1957) remarked on the difficulties in interpreting the mode of life of oncocerids and concluded that many of them were likely bottom dwellers, although he also admitted that there were probably swimmers and floaters among them. Furnish and Glenister (1964) interpreted oncocerids as predominantly benthic because of the proportionally small phragmocone, but they mentioned the possibility that some groups were nekto-benthic in view of the presence of a well-developed

hyponomic sinus. Similar statements were made by Frey (1989) and Teichert (1967). However, in agreement with Westermann (1973), we reject this interpretation because (1) the shell would be too big for a benthic animal without obvious benefit; (2) according to Clarke et al. (1979), there are four different solutions in extant cephalopods to achieve neutral buoyancy, of which a gas-filled phragmocone is just one and hence, there is no reason to assume that some nautiloids did not evolve another way of reducing their weight if the phragmocone alone was insufficient (such a mechanism was even suggested in oncocerids, see Niko and Nishida 2003; although their hypothesis has not been tested yet)—also considering the wealth of other organisms that evolved buoyancy mechanisms in many other different ways (in any case, non-functionality would probably cause an evolutionary reduction or loss of the phragmocone); (3) if the phragmocone was only used to slightly reduce the weight of the shell to ease carrying the shell or rapid escape movements, there would be no explanation for the enormous variability and complexity of the oncocerid siphuncle (e.g., Kröger 2003; Mutvei 2011, 2013).

Furthermore, contradicting statements were made by the same authors that advocated a benthic or nektobenthic lifestyle in that the short phragmocone chambers, large body chambers and possibly also the siphuncular structures were used to regulate buoyancy (Teichert 1967; Crick 1988; Frey 1989); so why would a primarily benthic animal need such a sophisticated buoyancy apparatus? Modern day *Nautilus* is only able to make very slight and slow adjustments to its buoyancy (Ward 1986) and actinosiphonate lamellae have been interpreted as increasing the efficiency of the siphuncle (Crick and Teichert 1979; Kröger 2003; Mutvei 2011). All these arguments suggest that oncocerids were well capable of living in the water column, possibly as vertical migrants (e.g., Kröger 2003; Mutvei 2011, 2013). However, because of the significant changes in apical angle and apertural contraction during ontogeny, the mode of life of juvenile oncocerids might have been quite different from that of adult individuals (Manda 2008; Manda and Frýda 2010).

Conclusions

We describe the new oncocerid genus *Basiloceras* with two species, *B. david* and *B. goliath*. Particularly the latter species attained a large conch size. Its conch could possibly reach a length of almost 1 m, but these dimensions are only rough estimates, as it strongly depends on the apical angle of the phragmocone, its changes during ontogeny, the shape and size of the apex and whether conch truncation

occurred as in some Silurian brevicones (see Stridsberg 1985).

Because of its huge size, it is not surprising that the empty conch was used by microconchids and various attached lophotrochozoans (brachiopods and possibly bivalves) as attachment surface (benthic island). Some specimens might alternatively have reached the conch by currents, where the empty conch functioned as a fossil trap. Some of the post mortem epicoles probably inhabited the inside of the empty body chamber and phragmocone, after some of the septa were broken or dissolved.

Both species of *Basiloceras* have a rather short body chamber. We discuss possible functions for the peculiar proportions and shape. In our opinion, body chamber proportions were in these cases mostly controlled by the requirements to maintain neutral buoyancy of this supposed vertical migrant. These hypotheses should be tested using quantitative volume models of oncocerid conchs in the future.

Systematic palaeontology

Class Cephalopoda Cuvier, 1797

Order Oncocerida Flower in Flower and Kummel, 1950

Family Acleistoceratidae Flower in Flower and Kummel, 1950

Remarks. *Basiloceras* is placed within the Acleistoceratidae based on its depressed exogastric breviconic conch shape, broadly expanded siphuncle and the lack of actinosiphonate lamellae (cf. Flower and Kummel 1950; Sweet 1964). However, the family-level classification of breviconic oncocerids needs revision and, therefore, some doubt remains regarding the family assignment. Dzik (1984) regarded the family as synonymous with the Brevicoceratidae Flower, 1941 (but assigned *Paracleistoceras* to the Jovellaniidae Foord, 1888), while other authors regarded the Acleistoceratidae as valid (e.g., Holland 2007; Gnoli and Serventi 2009).

Genus *Basiloceras* gen. nov.

Type species. *Basiloceras goliath* sp. nov.

Etymology. Basileus (Gr.) = king, referring to the large size of the type species and the groove near the peristome, reminiscent of a crown.

Species included. *Basiloceras goliath* sp. nov. and *Basiloceras david* sp. nov., both from the Middle Devonian of the Tafelalt.

Diagnosis. The conch is straight in the adult and subadult stage with a slightly depressed cross section. Towards the adult peristome, the cross section becomes subtriangular

with a distinctively flattened dorsum and a rounded venter. The body chamber is shorter than high and wide. It is contracted mainly on the dorsum and the venter, while the lateral sides are only slightly converging towards the aperture. Its aperture has a width of *c.* 0.8 and a height of *c.* 0.6 in relation to the maximal conch diameter at the base of the body chamber. The siphuncle is eccentric, close to the ventral side of the conch. The septal necks are cyrtocoanitic and the siphuncular segments broadly expanded, lacking actinosiphonate lamellae.

Discussion. *Basiloceras* is similar to *Paracleistoceras* Foerste, 1926 and *Acleistoceras* Hyatt, 1884 in general conch shape. However, it differs from both genera in the rounded subtriangular cross section of the body chamber and the convex dorsal outline, which is straight in *Paracleistoceras* and *Acleistoceras*. Furthermore, the conch of *Paracleistoceras* is clearly cyrtocoanitic, while it is more or less straight in *Basiloceras*, at least in the adult stage. The siphuncle of *Paracleistoceras* is located very close to the ventral side and contains continuous actinosiphonate lamellae, while it is removed from the shell wall by the distance of the siphuncular diameter in *Basiloceras* and lacks actinosiphonate lamellae at least in its adult stage. *Acleistoceras* differs furthermore in its longer body chamber and generally more elongate shape. Finally, the hyponomic sinus is smaller in *Acleistoceras*. *Calchasiceras* Shimansky, 1957 is similar in its short body chamber, but differs in its almost central siphuncle and the more oval cross section.

Remarks. In both species of *Basiloceras*, the juvenile part of the phragmocone is unknown. Presumably, it was curved exogastrically, as in the related *Acleistoceras*.

Basiloceras goliath sp. nov.

Figures 2, 4f–i, 5

Etymology. After Goliath, the biblical figure, referring to the large adult size.

Holotype. Body chamber with part of the phragmocone, PIMUZ 35927.

Type locality and horizon. Givetian strata near Rich Tamirant, between Oum El Hadej and El Khraouia, Tafilalet, Morocco (see Fig. 1a). The stratigraphic position was determined based on the faunal association of the specimen.

Material. Only the holotype.

Diagnosis. Very large *Basiloceras* that could reach an adult size of at least 180 mm in diameter. The aperture was probably reinforced by a thickened peristome, as indicated by distinct grooves parallel to the peristome on the internal

mould. The contraction of the body chamber is gradual, almost straight in lateral outline.

Description. The holotype PIMUZ 35927 consists of an internal mould of a nearly complete body chamber and eight partially eroded phragmocone chambers, but without any preserved shell remains. The conch is essentially straight, without a clear indication of curvature in the preserved part of the specimen. The specimen has a length of about 300 mm, a maximum width of 180 mm and a maximum height of 160 mm, both close to the base of the body chamber. The body chamber itself is 95 mm long and contracted. A broad hyponomic sinus is present, indicating the ventral side. The aperture is subtriangular with a width of 140 mm and a height of *c.* 100 mm, whereas the ventral part of the peristome is not completely traceable due to erosion. The dorsal side of the body chamber is distinctively flattened, while the ventral side is more rounded. The peristome has a rounded dorsal projection that reaches about 30 mm further anteriorly than the ventral side. Parallel to the dorsal projection is a groove at a distance of about 10 mm behind the aperture. The septal distance is 9 mm in the most adoral chamber and up to 15 mm in the adapical chambers, indicating septal crowding took place in the adult individual close to the cessation of growth.

Discussion. *Basiloceras goliath* differs from *B. david* sp. nov. in its much larger adult size. Furthermore, it has a less strongly contracted dorsum at the body chamber.

Remarks. Unfortunately, the position and the shape of the siphuncle are unclear in this species. However, the body chamber is morphologically so similar to *Basiloceras david*, thus suggesting a close relationship of the two species. Thus, we infer that the siphuncle of *B. goliath* is probably also located close to the ventral shell wall, a condition that is quite common in oncocerids. *B. goliath* was chosen as the type species because the body chamber of the holotype is better preserved and a larger portion of the phragmocone is available, thus better displaying the general conch shape.

Basiloceras david sp. nov.

Figures 4a–e, 6

Etymology. After David, the biblical figure, referring to the small size compared to the type species.

Holotype. Body chamber with a small part of the phragmocone, PIMUZ 35928.

Type locality and horizon. Jebel Ouafouil (Filon 12), middle Eifelian, *Subanarcestes macrocephalus* Zone (Fig. 1b).

Material. Only the holotype.

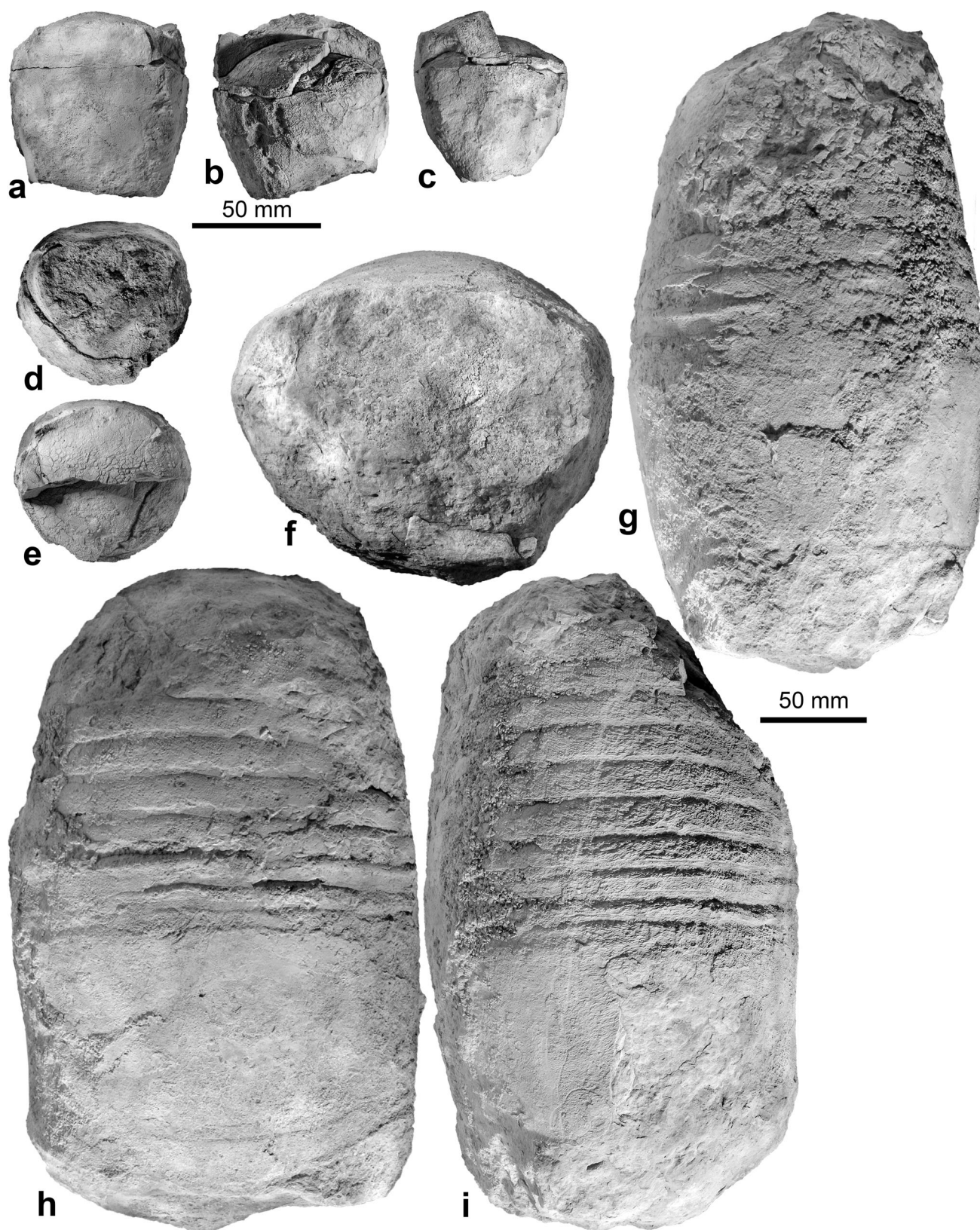


Fig. 4 *Basiloceras* gen. nov. All specimens were whitened with NH_4Cl . **a–e** *Basiloceras david* sp. nov., holotype, PIMUZ 35928, Eifelian, Jebel Ouauoufilal. Dorsal (**a**), ventral (**b**), lateral (dorsum left)

(**c**), adoral (**d**) and adapical (**e**) view. **f, i** *Basiloceras goliath* sp. nov., holotype, PIMUZ 35927, Givetian, SE of Oum El Hadej. Adoral (**f**), lateral (dorsum left) (**g**), dorsal (**h**) and ventral (**i**) view

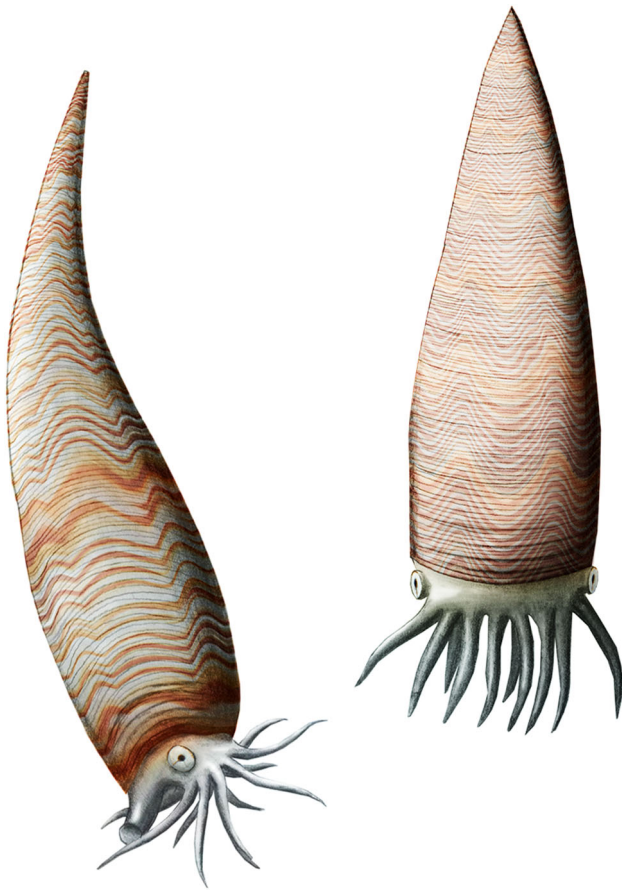


Fig. 5 Possible life reconstructions of *Basiloceras goliath* sp. nov. in lateral (left) and dorsal (right) view. Possibly, the phragmocone was straight and not slightly curved as shown here

Diagnosis. *Basiloceras* with a conch width of c. 80 mm at the base of the adult body chamber.

Description. The holotype PIMUZ 35928 is a body chamber with three partly preserved septa. It has a width of 78 mm and a height of 72 mm at the base of the body chamber. The entire specimen has a length of 80 mm, out of which 54 mm belong to the body chamber. Probably, the most adoral part of the body chamber is missing, but the slight change from a convex to a concave outline near the aperture and the amount of contraction indicate that likely only a small part is missing. The aperture has a rounded subtriangular shape, measuring 59 mm in width and 42 mm in height. The broad hyponomic sinus indicates the ventral side. The dorsum is distinctively flattened, while the venter is rounded. Both are convex in lateral outline, converging towards the aperture. The phragmocone chambers have a length of about 4–5 mm. The phragmocone has a width of 73 mm at the most adapical septum, 13 mm behind the base of the body chamber. The conch height is not discernible at the same position because the ventral parts of the septa are missing. Since only the most

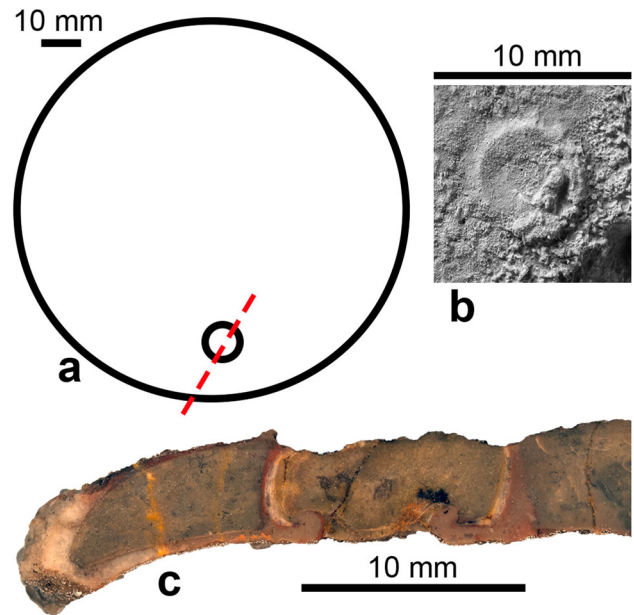


Fig. 6 Details of the siphuncle of *Basiloceras david* sp. nov., holotype, PIMUZ 35928. **a** Reconstructed outline of the last septum in adapical view, showing the position of the siphuncle and where the last chamber has been cut. **b** Detail of the siphuncle at the last septum with the last chamber removed, adapical view (whitened with NH_4Cl). **c** Polished section through the siphuncle (photographed under H_2O)

adoral chamber preserves a part of the siphuncle, the chamber was removed and obliquely cut as shown in Fig. 6a to study the structure of the siphuncle. The surface of the last septum—adoral of the removed septum—shows no traces of radial lamellae (Fig. 6b). The siphuncle has a circular cross section and is situated 9 mm away from the ventral shell wall. The siphuncular segment is broadly expanded with a maximum diameter of 12 mm and 4 mm at the septal foramen. The septal necks are cyrtocoanitic. Although the section is oblique to the plane of symmetry of the conch, the dorsal septal neck appears to be slightly closer to the connecting ring, which probably results from a scalariform siphuncle. The connecting ring is thick and consists of two layers: a thin outer layer of brown colour and a white inner layer.

Discussion: In addition to the above described differences to *Basiloceras goliath*, the holotype of *B. david* lacks the arched grooves near the aperture of the former. However, this could be due to the incomplete preservation or due to growth irregularities in the holotype of *B. goliath*.

Remarks. The shape of the body chamber corresponds well to the holotype of *B. goliath*, but the conch is much smaller. Large intraspecific variation of adult size is common in oncocerids and has in some cases been attributed to sexual dimorphism (Stridsberg 1985), but the stratigraphic gap and the very large size difference between *B. goliath*

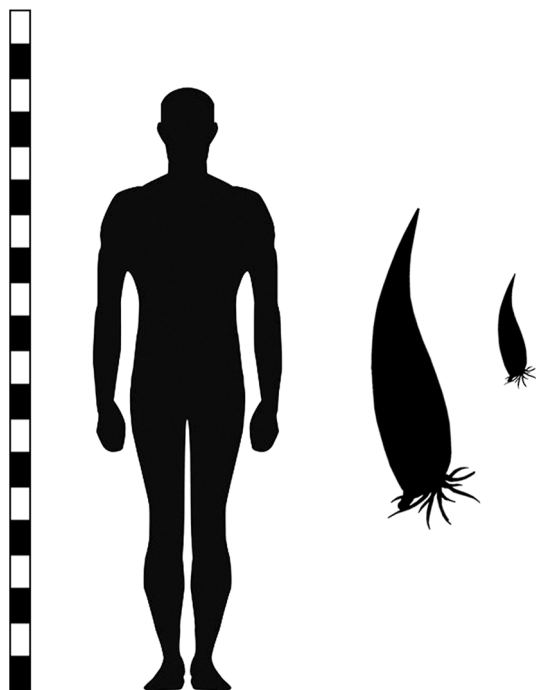


Fig. 7 Size reconstruction of *Basiloceras goliath* (middle) and *B. david* (right) compared to a human (left). Scale bar = 2 m

and *B. david* (Fig. 7) speak against the inclusion of both specimens in the same species, although we cannot rule this out with certainty.

Acknowledgements We thank the Swiss National Foundation for financial support (Project Number 200020_132870). We are thankful to the Ministère de l’Energie, des Mines, de l’Eau et de l’Environnement (Direction du Développement Minier, Division du Patrimoine, Rabat, Morocco) for providing working permits. Markus Hebeisen (Zürich, Switzerland) is thanked for advice for the preparation of the holotype of *Basiloceras goliath*. Said Oukherbouch (Tafraoute, Morocco) collected the large specimen and provided further information about its locality. We are grateful to Adam T. Halamski (Warszawa, Poland) for his help with the identification of the brachiopods and to Olev Vinn (Tartu, Estonia) for comments on the microconchids. Vojtěch Turek (Prague, Czech Republic) is acknowledged for showing us Barrande’s collection. We thank the reviewers David Evans (Peterborough, England), Štěpán Manda (Prague, Czech Republic) and Björn Kröger (Helsinki, Finland), whose comments helped to improve the manuscript. Daniel Marty (Basel, Switzerland) is thanked for his editorial work.

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