ORIENTATION OF CEPHALOPOD SHELLS IN ILLUSTRATIONS

by SVEN STRIDSBERG

ABSTRACT. Most drawings and photographs of fossil cephalopods show the shell upside down in respect to the animal's living position. As there is no advantage in this way of making illustrations, presumably based on tradition, the author suggests that fossil as well as living cephalopods should be illustrated in life position. This is particularly important today, as functional morphology is of vital interest to cephalopod workers. To facilitate understanding of the behaviour of fossil cephalopods, the first step must be to see them orientated in the same way as they saw each other.

ILLUSTRATIONS have always played an important role in palaeontological publications and it is of vital importance that they present material in a proper way. This applies to drawings as well as to photographs. All palaeontologists will agree with the above, but unfortunately we are, in some cases, still trapped in the traditional way of presenting illustrations.

In the last century when fossils were scientifically illustrated for the first time, it seems that aesthetics dictated their orientation. Regarding the cephalopods, evolute and involute specimens were normally illustrated with the body chamber on top of the shell in all lateral views. This might perhaps have been artistically satisfying, but it is definitely misleading for one trying to reconstruct the animal or study its functional morphology.

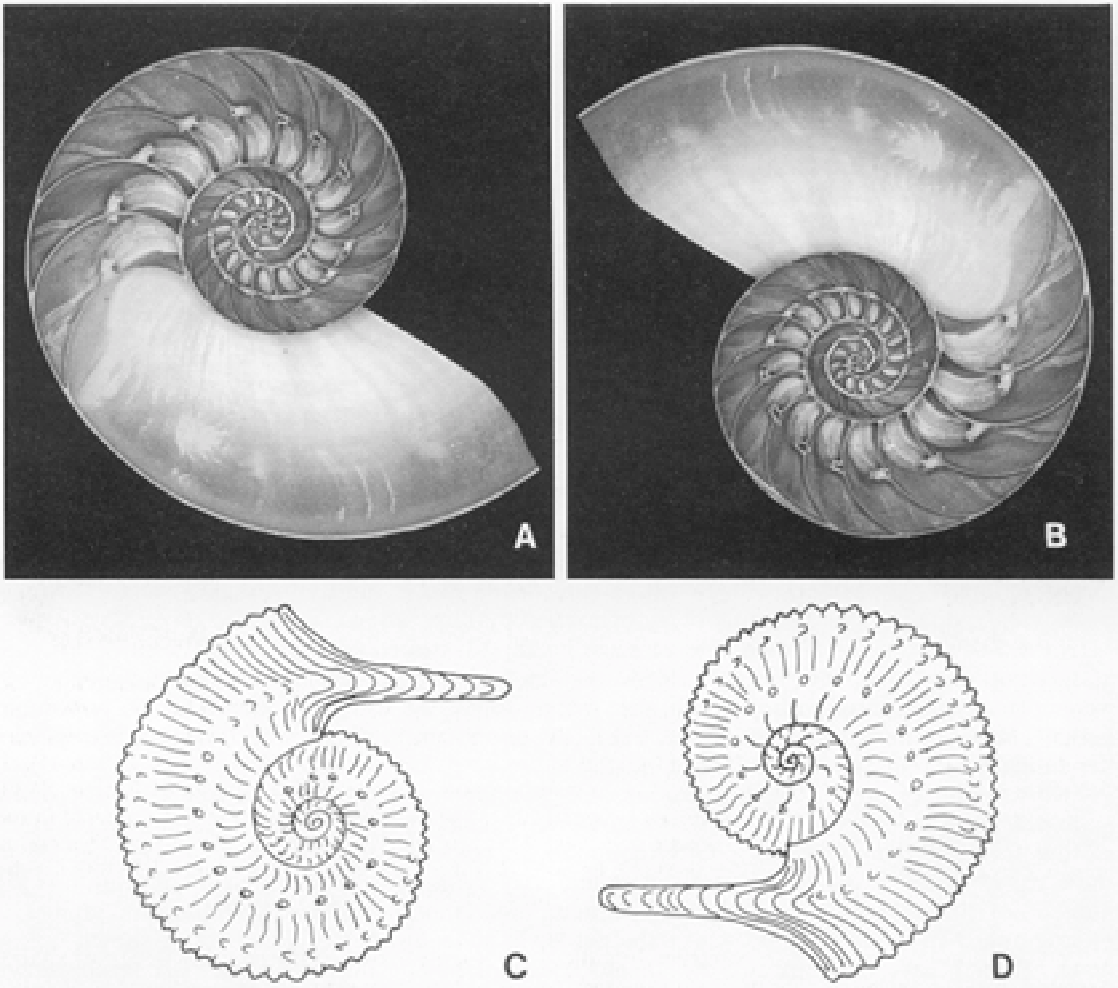
The tradition of presenting illustrations of cephalopods upside down, in respect to the living animal, is firmly established among palaeontologists. In many publications illustrating, for example, various forms of ammonites, it is fairly common for complementary drawings to be included to show the supposed living position of the animal. A very good example of such convention is the number of articles concerning the extant nautiloid, *Nautilus*, where the complete animal is photographed in living position whilst the cut shell, showing all the chambers, is shown upside down. Even I have been accused by an old friend of having illustrated *Nautilus* upside down (Stridsberg 1981, fig. 2), after he had studied the literature on the subject. All illustrations of *Nautilus* he could find showed the shell with the body chamber at the top of the shell. Now I find myself asking the same question (text-fig. 1) as he did: 'Why do they put it upside down?'.

The literature to which my friend referred was not only the popular variety but also palaeontology text-books and the *Treatise*. In the chapter 'Living *Nautilus*' in the latter (Stenzel 1964, pp. K59–K93) *Nautilus* is nicely illustrated in living position with soft parts (fig. 43) and upside down without soft parts (figs. 54–56). In all it is figured in ten pictures, five in living position and five upside down. I have asked before (Stridsberg 1985, p. 10) and I do so again. Who would dream of illustrating an *Australopithecus* upside down?

It must be in the interests of cephalopod workers to facilitate the understanding of all their readers, laymen as well as professionals, of the results they achieve, and not to use misleading methods. If anyone is in the position to interpret the correct living position it is the palaeontologist, and therefore we have a great responsibility to other readers.

Naturally it would be a break with tradition for many palaeontologists to see their material illustrated 'upside down' (in the old sense), but I strongly urge cephalopod workers to use common sense rather than to continue to follow old conventions. It might be confusing for those adhering to the 'old system' but I consider the present situation to be more confusing with all its possible combinations (text-fig. 2).

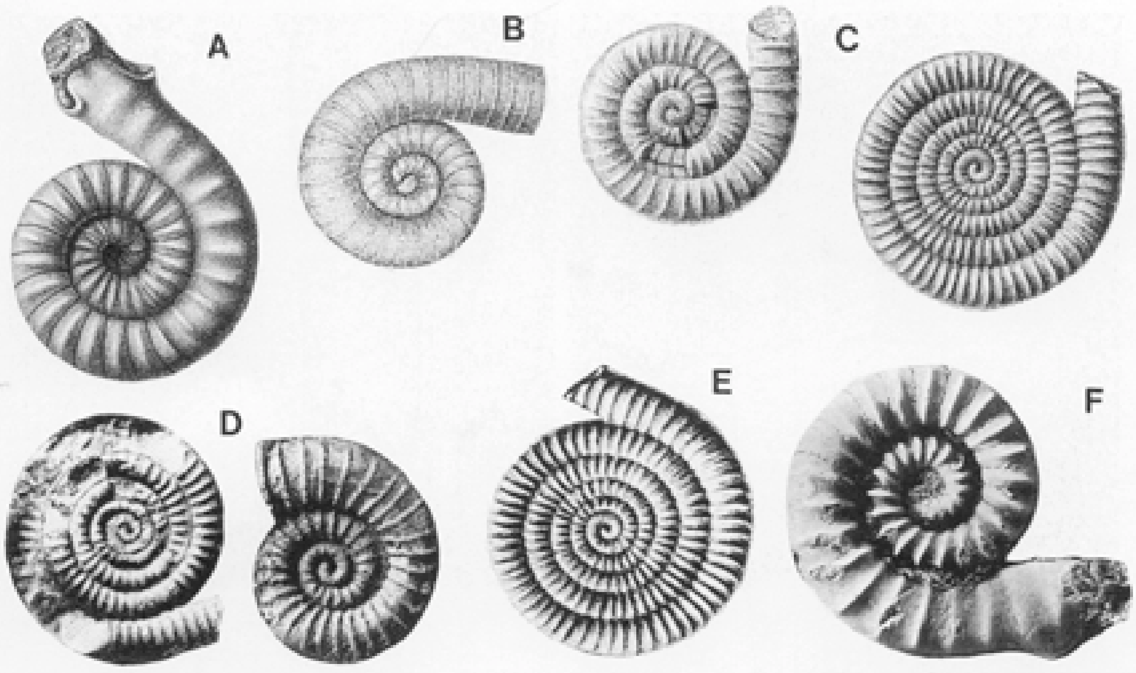
[Palaeontology, Vol. 33, Part 1, 1990, pp. 243–248.]



TEXT-FIG. 1. A, *Nautilus* shell in living position. B, *Nautilus* upside down. What makes B look more attractive than A? C and D, the ammonite *Kosmoceras* in common publication mode (C) and in living position (D).

However, there is a problem in reconstructing the living position in incomplete involute or evolute cephalopods as the only indicator of up-and-down is the position of the body chamber. In ammonites where there is good reason to believe that only the body chamber is missing due to the lack of the reinforcements the septa make to the phragmocone, the end of the whorl might as well be orientated at the lower part of the shell as at the upper. This suggestion is based on the fact that the body chamber in ammonites often occupies roughly a whole whorl of the shell. In similarly shaped nautiloids with missing body chamber, variation is great between various taxa. In *Ophioceras* for example the body chamber will occupy almost a whole whorl, while *Nautilus* has a body chamber occupying only about a third of a whorl. Nevertheless the seeker of perfection must always try to reconstruct the orientation of the specimen under consideration. Naturally due to lack of information incomplete specimens might be incorrectly orientated in the future but that is not an argument for ignoring the problem.

An advanced and accurate method on how to reconstruct the life orientation of fossil cephalopods is demonstrated by Okamoto (1988), who investigated some heteromorph ammonoids.

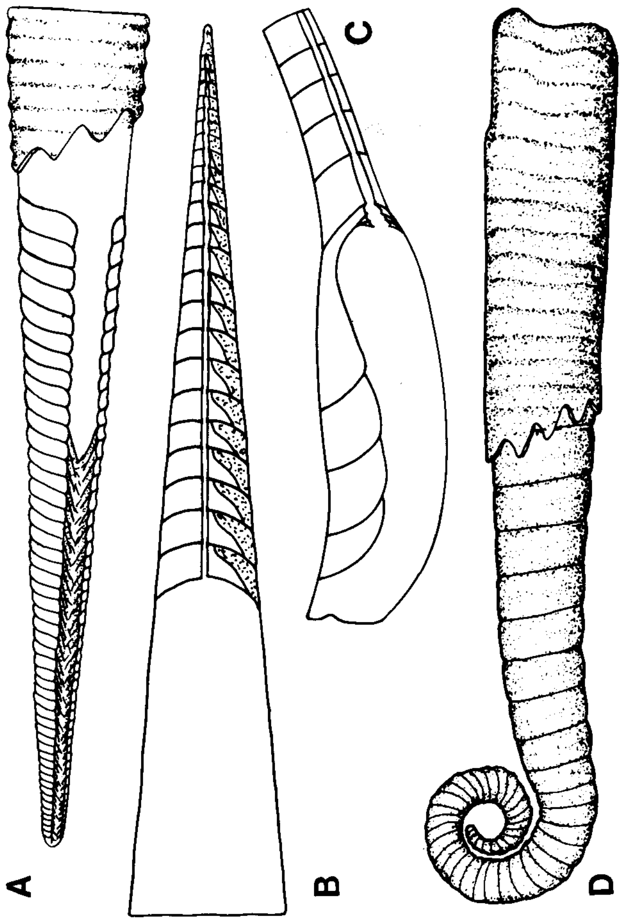


TEXT-FIG. 2. Illustrations of *Ophioceras* from six publications demonstrating various orientations: A, *Ophioceras simplex* Barrande 1865, as figured by Barrande (1865, pl. 97, fig. 2). B, *Ophidioceras reticulatum* Angelin 1880, as figured by Angelin (Angelin and Lindström 1880, tab. 16, fig. 1). C, *Ophidioceras reticulatum* Angelin 1880 and *Ophidioceras rota* Lindström 1890 as figured by Lindström (1890, pl. 7, figs. 29 and 34). D, *Ophidioceras welleri* Foerste 1930 and *Ophidioceras wilmingtonense* Foerste 1925 as figured by Foerste (1930, pl. 25, figs. 5 and 6). E, *Ophioceras reticulatum* (Angelin 1880), the same illustration as in C but figured in the Treatise in the same position as Barrande's *O. simplex* (A) (Furnish *et al.* 1964*b*, fig. 270: 1b). F, *Ophioceras simplex* Barrande 1865 as figured by Turek (1972, fig. 3). Apart from one of Foerste's figures (D (5)) this is the only illustration figuring a specimen of *Ophioceras* (*Ophidioceras*) in living position.

The shells from these animals are extremely difficult to orientate due to their highly irregular shape. Assisted by a computer, Okamoto managed to reconstruct extremely well not only the life orientation of adult animals but also changes in life orientation during their ontogeny (Okamoto 1988, text-fig. 6). Naturally this computer method is also available for other cephalopods and similar investigations with symmetric shells will be less complicated. Hopefully there will soon be more investigations employing computer orientations, and this will increase the demand for standardization of cephalopod illustrations.

Unfortunately it is not only evolute or involute cephalopods which are treated in an unfair way, but also many of the orthocones. In a palaeoecological paper, Flower (1957; pp. 829–852) discussed the horizontal floating position of various kinds. He (Flower 1957, figs. 2–6) demonstrated from the disposition of internal deposits the resulting floating orientations of the animals. Three of his illustrations (Flower 1957, figs. 4–6) have become classical and have been republished several times as they show very clearly the orthocone floating mechanism (see also Flower 1955, p. 246).

The deposits found in orthocones are located in the apical chambers, in the siphuncle, or in both areas. They do not completely fill the apical chambers but are concentrated on the ventral side of the shell to help the animal maintain stability. Strictly speaking they served more or less as ballast, to keep longitudinal as well as rotational stability. In those genera where the deposits were concentrated in the siphuncle, this was not situated in the centre of the shell but was ventral, or ventrally to the centre, to obtain the same result, viz. maintenance of stability.



TEXT-FIG. 3. This text-fig intentionally illustrates four longicones in vertical orientation in a full page figure, as if they were too long to be illustrated horizontally. All specimens have a defined floating position and have their dorsal side towards the left. A, *Endoceras* with siphuncular deposits, indicating what is dorsal and ventral. B, *Orthoceras* with ventral deposits in the closed chambers. C, in this nearly mature *Glossoceras* the dorsally located gas chambers serve to keep the shell in balance. D, the gas-filled apical end of *Lituites* keeps the dorsal side of the shell upwards.

As orthocones with cameral or siphuncular deposits, have a defined living position, there is no reason to illustrate these shells with the ventral side upwards. As soon as we can decide what is dorsal and what is ventral, there should be no hesitation in showing this in illustrations (text-fig. 3).

In some groups of more or less straight cephalopods with a horizontal living position, stability was not accomplished by ventral deposits, but by dorsally located gas chambers. In *Lituites* the coiled apical end of the shell served as a stabilizer (text-fig. 3D) and in *Glossoceras* the dorsally located gas chambers in the mature animal kept the shell in balance (Furnish *et al.* 1964*a*, fig. 190C).

Regarding the orthocones and other long shells, it is sometimes not practically possible to print lateral views in a proper way as the length of the shell favours a vertical reproduction. 'By tradition' the apical end has been located mostly to the top of the page. Again, however, it must be emphasized that all lateral views of orthocones, orientated along the page, should be figured with the dorsal side in the same direction, here suggested to the left, regardless of whether the apical end will be located at the top or the bottom of the page. This will facilitate the reader to understand the illustration when turning the figure to place the orthocones horizontally.

A good example of illustrating a cephalopod in a proper way is the reconstruction of the ascocerid, *Glossoceras lindstroemi* Miller in the *Treatise* (Furnish *et al.* 1964*a*, figs. 190–191). However, in the following figures in the chapter the authors have chosen to place all specimens with the apical end in the same direction, and thus some specimens are illustrated with the dorsal side to the right and some with the dorsal side to the left (e.g. fig. 196: 1b and 2b respectively). The authors have been consistent in making their illustrations and all shells have the same orientation, although some shells are not placed correctly based on functional morphology. If all shells had been orientated with the dorsal side up, or at least to the left, it would have facilitated comparison of different specimens.

The brevicone nautiloids comprise another group carefully illustrated upside down. As the cameral part of the shell acted as the lifting device and the body chamber the sinking device, I can see no reason for figuring these shells with the apical end downwards. In this case it is probably a heritage from Barrande, who made numerous illustrations of rich material (Barrande 1865, 1866). As some of these groups had interesting apertural openings, the material was reproduced upside down several times, just as in Barrande's work. I recommend that in the future such specimens ought to be figured with the apical end upwards. I have illustrated brevicone nautiloids (Stridsberg 1985, 1988*a* and *b*), in what I believe is the living position and one comment in a review was 'it will be normal if you turn the page over'.

I believe it would be better for us to overturn the old way of making cephalopod illustrations, rather than to leave it to future readers. In summary I strongly recommend that cephalopods are illustrated according to inferred life position, and I hope that this paper will stimulate fruitful discussion on this topic among cephalopod workers.

Acknowledgements. For valuable comments on this controversial subject I am most thankful to Charles H. Holland, Dublin, and Lennart Jeppsson, Lund. Thanks to, or due to, their encouragement, I decided to finish this paper. I also thank Ingrid Sawers for improving the English and Claes Bergman for drawing A and D in text-fig. 3.

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Typescript received 21 September 1988
Revised typescript received 25 April 1989