MORPHOLOGY AND TAXONOMIC STATUS OF THE JURASSIC BELEMNITE *'RHOPALOTEUTHIS' SOMALIENSIS* SPATH 1935

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ABSTRACT. The new genus *Somalibelus* is erected, type species *Rhopaloteuthis somaliensis* Spath 1935. The external and internal morphology of the species is described in detail using material from the type locality in the Kimmeridgian of Somalia, Africa. All the material studied is regarded as belonging to a single, highly variable species. The ontogeny and limits of variation of the species are discussed.

THE original diagnosis of *Rhopaloteuthis somaliensis* (Spath 1935, p. 223) points out the ventral position of the median alveolar groove (canal) which extends on its alveolar part. This statement is incompatible with the reference of this species to the genus *Rhopaloteuthis* and family Duvaliidae Pavlow 1914, which are characterized by the dorsal position of this groove. This had induced the writer (Jeletzky 1966, pp. 123, 124, 128) to place '*R.*' *somaliensis* into the belemnopseid genus *Curtohibolites* Stoyanova-Vergilova 1963. A subsequent, more detailed study of the original material of '*R.*' *somaliensis* including its type specimens necessitated a reappraisal of this assignment, the results of which are presented below.

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Abbreviations. Repositories of specimens are indicated as follows: S.M.C., Sedgwick Museum, Cambridge; B.M.N.H., British Museum (Natural History).

SYSTEMATIC DESCRIPTION

Family BELEMNOPSEIDAE Naef, 1921 emend. Jeletzky, 1946

Genus SOMALIBELUS nov.

Type species. *Rhopaloteuthis somaliensis* Spath 1935

Diagnosis. A *Curtohibolites*-like guard characterized by a distinctly addorsally displaced, more or less distinctly oval to egg-shaped, dorso-ventrally elongated alveolus, absence of double lateral furrows, and the presence of single mediolateral longitudinal ridges flanked by flattened to slightly depressed, narrow longitudinal zones on one or

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two sides; splitting surface even but more or less rough-surfaced except in a narrow zone adjoining the ventral side of the alveolus and in the adoralmost part of the guard.

Geographical range. Somalia, formerly Somaliland Protectorate (British Somaliland), Africa.

Stratigraphic range. Kimmeridgian (lower?; or middle?; compare Spath 1935, pp. 219, 223).

Historical remarks. The original placement of *Somalibelus somaliensis* in the duvaliid genus *Rhopaloteuthis* was caused by the long-standing controversy about the taxonomic status of this genus recently reviewed by Pugaczewska (1957, pp. 385–386) and Gustomessov and Uspenskaya (1968, pp. 65–67).

Spath (1933, pp. 664, 665; 1935, p. 219) was fully aware of the fact that the siphuncle of the *S. somaliensis* is situated on the same side of the guard as the medioalveolar groove. He nevertheless placed it in the genus *Rhopaloteuthis* Lissajous 1915 believing Lissajous's (1915, 1925, pp. 41–42, text-fig. 23) conclusions about the dorsal position of the alveolar canal in its genotype *R. sauvanaui* (d'Orbigny) to be in error. Spath (loc. cit.) believed that *Rhopaloteuthis* is characterized by the ventral position of alveolar canal in contrast to *Conobelus* Stolley 1919 which is characterized by its mediodorsal position. These conclusions were subsequently discredited by work of Pugaczewska (1957, pp. 385–386), Jeletzky (1966, p. 144 and unpublished observations on original material of *R. sauvanaui*) and Gustomessov and Uspenskaya (1968, pp. 65–67).

'*R.*' *somaliensis* Spath 1935 is extremely similar to representatives of the recently erected mid-Lower Cretaceous genus *Curtohibolites* Stoyanova-Vergilova 1963 in the external morphology of its guard. Like '*R.*' *somaliensis*, all *Curtohibolites* species are characterized by the presence of a medioventral canal on the alveolar part of the guard. For these reasons '*R.*' *somaliensis* was transferred into *Curtohibolites* by Jeletzky (1966, pp. 123, 124, 128) following the recognition of the duvaliid nature of *Rhopaloteuthis*, in spite of its considerably older (lower or middle Kimmeridgian) age. A subsequent, more detailed study of external and internal morphology of a representative sample of '*R.*' *somaliensis*, including its type specimens, revealed a number of important morphological distinctions from *Curtohibolites* and all other genera of Belemnopseidae. These morphological distinctions necessitate the erection of a new genus for '*R.*' *somaliensis* and suggest its being an older, more primitive homoeomorph of *Curtohibolites* (see below).

Affinities and differences. As already mentioned, the external morphology of *Somalibelus* resembles closely that of the genus *Curtohibolites* as interpreted by the type species *C. trubatchensis* Stoyanova-Vergilova 1963. However, it differs from *Curtohibolites* in the following taxonomically important morphological characters:

1. The guard of *C. trubatchensis* is characteristically feebly compressed in the anterior part but feebly depressed in its apical part.
2. The splitting surface of *C. trubatchensis* is smooth throughout and has a different shape. Its bottom runs in a straight line obliquely adapically in the inner half of the guard's cross-section (Stoyanova-Vergilova 1963, p. 213, text-fig. 2). Then it turns abruptly and runs obliquely adorally in a straight line until it reaches the ventral surface of the guard a few mm adorally of the protoconch's level.
3. Double lateral lines are characteristically present in *C. trubatchensis*. They are well developed to incised, closely spaced, subparallel and strongly displaced adventrally in the alveolar part of the guard.

4. The position of the alveolus in relation to the guard's axis is not mentioned either in the description of *C. trubatchensis* or in that of any other species placed in *Curtohibolites* by Stoyanova-Vergilova (1963). However, the poor figures provided by her (Stoyanova-Vergilova 1963, pl. II, figs. 1*c*, *d*, *e*, 2*c*, 5*c*, *d*, *e*, 6, 7*c*, *d*) are enough to attest its central position at least in *C. trubatchensis* and *C. wernsdorfensis*. The same appears to be true of the alveolus of the still less satisfactorily reproduced *C. rasgradensis* and *C. orbignyanus* Stoyanova-Vergilova 1963 non Duval-Jouve 1841 (see Stoyanova-Vergilova 1963, pl. I, figs. 1*d*, 2*c*, *d*, 3*c*, 4*c*, *d*, *e*).

These morphological distinctions appear to be ample for the recognition of generic independence of *Somalibelus somaliensis* (Spath 1935) from *Curtohibolites*.

S. somaliensis (Spath 1935) resembles representatives of *Parahibolites* Stolley 1919 in the characteristic feeble to marked compression of its guard. It differs markedly from all representatives of *Parahibolites*, however, in the addorsal displacement of the alveolus, an entirely different character and outline of the splitting surface, absence of double lateral furrows, presence of single lateral ridges, and the compressed cross-section of the phragmocone.

The compression of the guards of *Somalibelus* and *Parahibolites* must, therefore, be the result of homoeomorphy rather than of a direct genetic link between these otherwise dissimilar Belemnopseidae genera.

From all representatives of genera *Belemnopsis* Bayle 1878, *Hibolithes* Montford 1808, *Mesohibolites* Stolley 1919, and *Neohibolites* Stolley 1919, *S. somaliensis* (Spath 1935) differs in the same morphological features as from the representatives of *Parahibolites*. The guards of the former four genera are, besides, characteristically depressed in their postalveolar parts at least, which contrasts with the more or less compressed cross-section of the corresponding part of the *S. somaliensis* guard. Even the exceptional representatives of *Belemnopsis* (e.g. *B. angusta* Stolley 1919, *B. mackayi* Stevens 1963, *B.* ex gr. *uhligi* Stevens 1963) and *Hibolithes* (*H. beyrichi* Oppel) characterized by equidimensional to somewhat compressed cross-sections of the posterior parts of their guards differ sharply from *S. somaliensis* in all other above-mentioned features. This leaves no doubt about generic independence of *S. somaliensis* from the four above-mentioned belemnopseid genera.

All known representatives of *Pseudohibolites* Blüthgen 1936 differ sharply from *S. somaliensis* in the complete absence of medioventral canal and splitting surface on the preserved alveolar parts of their guards (Blüthgen 1936, p. 40). Furthermore, they possess strongly developed single lateral furrows on the anterior parts of the flanks which may merge into double lateral furrows on the posterior parts of the flanks. At the same time they lack the characteristic single longitudinal ridges of *S. somaliensis*. These morphological distinctions are of a familial rather than generic rank in the writer's opinion.

Genetic ties of Somalibelus. Among the Belemnopseidae *Somalibelus* resembles most closely the unusually short, sturdy, and laterally compressed representatives of *Belemnopsis* (e.g. *B.* ex gr. *angusta-apiciconus*) occurring in the late early Bajocian and middle Bajocian of Normandy (Stolley 1927, p. 123, pl. 24, fig. 9; Eudes-Deslongchamps, 1878, pp. 69–73, pl. VII, figs. 1–4). In addition to the general similarity of the cross-section, shape, and proportions of the guard, *Belemnopsis angusta* Stolley resembles *S. somali-*

ensis in the indistinctness or complete absence of double lateral furrows. In spite of these points of similarity and suitable stratigraphic relationships, it is impossible to interpret *S. somaliensis* as a direct descendant of *B.* ex gr. *angusta-apiciconus*. All known representatives of this species group possess a differently shaped, completely smooth splitting surface closely resembling that of *Hibolithes jaculum* Phillips or *H. inflexus* Stolley (Krymgolts 1939, p. 12, pl. I, fig. 2*b*; text-figs. 1, 5). This splitting surface begins slightly adapically of the protoconch and its bottom extends obliquely apically and ventrally until it reaches the ventral surface of the guard somewhat below its middle. The presence of a considerably more advanced, completely smooth splitting surface already in the oldest known Bajocian *Belemnopsis* forms suggests that *Somalibelus* evolved directly out of some still unknown morphologically similar but older and morphologically more primitive belemnopseids transitional between *Hastites* ex gr. *clavatus lanceolatus* Hartmann 1830 on the one hand (Jeletzky 1966, pp. 143, 144), and *Belemnopsis* ex gr. *angusta-apiciconus* on the other. This hypothesis agrees well with the distinctly primitive *Hastites*-like ontogenetic development of the guard of *S. somaliensis* discussed below.

It seems probable that the main stem of Belemnopseidae represented by the *Hibolithes*- and *Belemnopsis*-like forms repeatedly produced more or less short-lived, specialized offshoots characterized by unusually sturdy guards (e.g. *Belemnopsis* ex gr. *angusta-apiciconus*, *Somalibelus*, *Curtohibolites*). These offshoots may have been adaptations to a less active, nektobentonic mode of life in closer proximity to the shoreline in comparison with the more typical, slender, and subfusiform representatives of the family.

Somalibelus somaliensis (Spath 1935)

Plates 30–38

1929 *Belemnites (Belemnopsis) sauvanaui* d'Orbigny; Weir, p. 18, pl. III, fig. 5.
1933 *Rhopaloteuthis (Belemnopsis) sauvanaui* (d'Orbigny); Spath, p. 665.
1935 *Rhopaloteuthis somaliensis* Spath, pp. 223–224, pl. XXV, figs. 4*a*, *b*.

Type specimens. Spath (1935, p. 223) has expressly designated the only figured, fragmentary specimen of *R. somaliensis* as its holotype. This choice is most unfortunate on two counts. Firstly, the selected holotype (C. 42147; Spath 1935, pl. III, fig. 5) consists of one half of the guard only and even this fragment lacks a few mm at the apical end. It is, therefore, impossible to observe a number of taxonomically important morphological features in the holotype (e.g. the medioventral canal, character of the apical end, shape of the guard in ventral aspect). Secondly, the holotype does not represent the average form of the species but one of its extreme variants; namely the extremely sturdy and apically obtuse form with an extremely deep alveolus. Such forms are by no means common in the population sample studied and the unfigured paratype II of Spath (1935, p. 223; this paper, Pl. 31, fig. 2) is undoubtedly much more representative of *S. somaliensis*. The unfigured paratype I of Spath (1935, p. 223; this paper Pl. 31, fig. 3) appears to be extremely close to the holotype in all taxonomically important features including the depth of its alveolus.

The unfigured holotype of *R. somaliensis* var. *attenuata* (Spath 1935, p. 223) is reproduced in Pl. 31, fig. 1 of this paper. This reasonably complete and satisfactorily preserved guard is morphologically representative of another extreme variant of the species characterized by relatively slender, markedly laterally compressed guard with a shallow alveolus (Pl. 30, fig. 6; Pl. 32, fig. 3).

Material studied. This revision of '*R.*' *somaliensis* is based on a detailed study of about 85 satisfactorily to well preserved, fragmentary to almost complete guards from the type locality preserved in collections of the Sedgwick Museum, University of Cambridge, England. The holotype of the species, that of '*R.*' *s.* var. *attenuata*, and two unfigured paratypes (Spath 1935, p. 223), preserved in collections of the British Museum (Natural History) were also restudied. A considerable number of other topotypes of '*R.*' *somaliensis* preserved in these collections were not studied in any detail as they did not seem to be any different from the Sedgwick Museum material.

External morphology. The guard is small, short to very short and sturdy. The estimated length of the largest known representative (C. 45936; Pl. 31, fig. 3) is about 33 mm. The estimated elongation of the guard (i.e. the ratio of estimated length to the maximum dorso-ventral diameter) fluctuates between 3 and 4·5 in the best preserved specimens. The critical measurements and ratios of best preserved and most complete guards are summarized in Table 1. As a rule, the guard is more or less distinctly subclavate, more markedly so in ventral than in lateral aspect. In ventral aspect, the shape of undistorted guards varies from slightly (Pl. 30, fig. 5*a*) to markedly (Pl. 32, fig. 2*a*, *d*) subclavate. The maximum lateral diameter is mostly situated within the apical half of the guard closely above or closely below the apex of the alveolus. This applies to sturdy individuals similar to the holotype of the species (Pl. 30, figs. 3*a*, 5*a*; Pl. 31, figs. 3*a*, 4*a*) and to slender forms similar to its var. *attenuata* (Pl. 31, fig. 1*a*, *b*; Pl. 32, figs. 2*a*, *d*, 3*a*, *d*). Some exceptional guards are, however, almost cylindrical in ventral aspect (Pl. 30, figs. 6*a*, *c*, 7*a*, *c*). In these aberrant specimens the almost unnoticeable maximum swelling of the guard occurs either in its middle or slightly adorally therefrom.

EXPLANATION OF PLATE 30

Somalibelus somaliensis (Spath 1935). Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa. Exact horizon and location unknown; the specimens may have been collected at different spots near Bihendula (Spath 1935, pp. 219, 224). Letter V marks the position of ventral side of guard.

Figs. 1*a*–*e*. SMC F. 13456/9. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view, ×1; *d*, Same view as in 1*c*, ×4; *e*, Alveolar view, ×10 showing addorsal displacement of the alveolus and the siphuncle (marked s).

Figs. 2*a*, *b*. SMC F. 13456/20. Fragment of the alveolar part of the guard, polished at both ends. *a*, Adapical cross-section, ×4; *b*, Adoral cross-section, ×4.

Figs. 3*a*–*c*. SMC F. 1690. *a*, Ventral view, ×1; *b*, Right lateral view, ×1; *c*, Left lateral view of phragmocone and splitting surface (marked sps), with left half of guard removed, ×4.

Figs. 4*a*–*d*. SMC F. 13456/12. Fragment of the alveolar part of the guard, polished at the adoral end. *a*, Ventral view, ×1; *b*, Right lateral view, ×1; *c*, Adoral cross-section (polished), ×4; *d*, Adapical cross-section, ×1.

Figs. 5*a*–*e*. SMC 297. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view with oral half of right side of guard (broken piece) removed, ×1; *d*, Right lateral view of phragmocone and splitting surface, same view as in 5*c*, ×4. Note contrast between the almost to quite level and partly smooth appearance of splitting surface (marked sps) and the rough surfaced appearance of the dorsal part of the guard. *e*, Alveolar view, ×1.

Figs. 6*a*–*e*. SMC F. 13456/21. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Same view as 6*a*, ×3; *d*, Right lateral view, ×3; *e*, Alveolar view, ×3; *f*, Apical view, ×3.

Figs. 7*a*–*f*. SMC F. 13456/15. *a*, Ventral view, ×1; *b*, Right lateral view, ×1; *c*, Same view as in 7*a*, ×2·5; *d*, Same view as in 7*b*, ×2·5; *e*, Alveolar view, ×2·5; *f*, Apical view, ×2·5.

In most undistorted specimens the guard contracts slightly and more or less evenly all the way adorally from the level of its maximum lateral diameter. In a few specimens (e.g. Pl. 32, fig. 2*a*, *d*) this even and regular adoral tapering is interrupted by a feeble constriction of the guard restricted to the lower part of the alveolar region. This results in a feebly concave ventral outline of the alveolar parts of such specimens which is unlike the essentially straight ventral outlines of the majority of specimens.

Adapically of the level of maximum lateral diameter most guards contract considerably faster in the ventral aspect than they do adorally therefrom. In many guards morphologically similar to the holotype of the species the contraction increases progressively to the apex (Pl. 30, figs. 3*a*, 5*a*; Pl. 31, figs. 3*a*, 4*a*; Pl. 32, fig. 4*a*). This results in a pronouncedly convex and obtuse (apical angle from 90 to 120°) apical end of the guard in ventral aspect. A small, mostly poorly defined, mucro may be superimposed on the broadly rounded base of the apical end in some of these specimens (Pl. 31, fig. 3*a*).

In a considerable number of other specimens either similar to *S. s.* var. *attenuata* (Pl. 31, fig. 1*a*, *c*; Pl. 32, figs. 2*a*, *d*, 3*a*, *d*) in the degree of their slenderness or approaching the holotype of the species in their sturdy proportions (Pl. 30, fig. 1*a*; Pl. 31, fig. 2*a*, *d*) the initially slight and gradual adapical tapering of the guard increases more or less abruptly within its apical quarter. Further adapically the flanks of such guards converge at angles ranging from about 30° (Pl. 32, fig. 3*a*, *d*) to about 60° (Pl. 31, fig. 2*a*, *d*) to the apex which results in an essentially straight, conical ventral outline of the apical quarters.

Some of the previously mentioned slender guards (Pl. 30, figs. 6*a*, *c*, 7*a*, *c*), in which the maximum lateral diameter is situated either in the middle of the guard or slightly higher, contract gradually and increasingly right through the lower two-thirds of their length. This results in the obtusely rounded, distinctly mucronate appearance of the apex in some of these slender (laterally subconical; see below) guards (Pl. 30, fig. 6*a*–*d*). Numerous transitional forms (e.g. Pl. 32, fig. 2*a*, *d*) connect the above described extreme forms with one another.

The lateral outline of many undistorted specimens is shaped similarly to their ventral outline except for a lesser degree of adapical and adoral contraction. This is true of most of the slender specimens approaching var. *attenuata* (Pl. 31, fig. 1*b*, *e*; Pl. 32, fig. 3*b*, *c*) but also applies to a number of sturdy guards including the holotype (e.g. Pl. 31, fig. 2*b*, *c*, *e*, *f*; Pl. 32, fig. 5*a*–*d*). However, a considerable number of sturdy specimens approaching the holotype (e.g. Pl. 30, figs. 1*b*, *c*, *d*, 3*b*, 5*b*; Pl. 31, fig. 4*b*, *c*) are almost cylindrical in lateral aspect, except for their obtusely rounded (and sometimes mucronated) to conical apical quarters, the outlines of which remain entirely similar to the already discussed ventral outlines of the apical quarters of the same specimens.

The lateral outlines of some of the previously mentioned ventrally subcylindrical guards (e.g. Pl. 30, fig. 7*b*, *d*) are entirely similar to their ventral outlines. Those of some other ventrally subcylindrical guards (e.g. Pl. 30, fig. 6*b*, *d*) taper adapically throughout their length. This results in the high conical lateral outline of such guards. The lateral outlines of their apical quarters may either be obtusely rounded and mucronate because of a progressive increase of contraction in this direction (Pl. 30, fig. 6*b*, *d*) or acute and wedge-shaped (Pl. 30, fig. 7*b*, *d*).

The alveolar cross-sections of all undeformed guards vary from feebly to markedly compressed and from more or less regularly elliptical to distinctly laterally flattened (Pl. 30, figs. 1*e*, 2*a*, *b*, 4*c*, 5*e*, 6*e*, 7*e*; Pl. 31, figs. 1*f*, 2*g*, 4*e*; Pl. 32, fig. 4*d*). Among these alveolar cross-sections, those of the sturdiest guards approaching the holotype of the species (e.g. Pl. 30, fig. 1*e*; Pl. 31, figs. 2*g*, 4*e*) are characterized by the least amount of compression (ratio lateral diameter/dorso-ventral diameter from 0·86 to 0·88) and almost regularly rounded flanks, while those of the relatively slender guards approaching var. *attenuata* in this respect (e.g. Pl. 30, fig. 7*e*; Pl. 31, fig. 1*f*) are the most compressed (the ratio lateral diameter/dorso-ventral diameter fluctuates from 0·84 to 0·86) and possess distinctly to markedly flattened flanks.

Most of the slender forms approaching var. *attenuata* (Pl. 30, figs. 2*a*, 6*f*, 7*f*; Pl. 31, fig. 1*g*; Pl. 32, fig. 3*f*) remain feebly laterally compressed all the way adapically and retain the above described elliptical but more or less laterally flattened cross-section throughout the posterior two-thirds of the guard. However, in a few slender guards like that reproduced in Pl. 32, fig. 2, the compression decreases adapically and finally disappears at the level about 11·5 mm above apex where the dorso-ventral and lateral diameters are about 5·9 mm each. Further adapically the cross-sections of this guard remain about equidimensional in spite of the ventral surface becoming somewhat flattened in the middle (Pl. 32, fig. 2*g*).

The shape and proportions of cross-sections within the posterior half to one-third of the guard vary ordinarily from distinctly compressed and feebly laterally flattened cross-sections (Pl. 31, fig. 1*g*; Pl. 32, fig. 4*e*) to either slightly compressed (e.g. the unfigured specimen F 1689 with the compression ratio of maximum lateral diameter/maximum dorso-ventral diameter of 8·0/8·4 = 0·95) or more or less equidimensional and regularly rounded cross-sections (Pl. 31, fig. 3*g*); Pl. 32, fig. 2*g*). The posterior cross-sections of another fairly numerous group of specimens are more or less equidimensional but rounded-subtrapezoidal with the maximum lateral diameter displaced adventrally (Pl. 31, figs. 2*h*, 4*f*). The about equidimensional regularly rounded and rounded-subtrapezoidal cross-sections are prevalent among the sturdy representatives of *S. somaliensis*. They appear to be about equally common in this form group. However, there are some sturdy representatives of *S. somaliensis* the cross-sections of which remain

EXPLANATION OF PLATE 31

Somalibelus somaliensis (Spath 1935). Horizon and locality as for Plate 30. V marks the position of the ventral side of the guard.

Figs. 1*a*–*g*. BMNH C. 42146. Holotype of *Rhopaloteuthis somaliensis* var. *attenuata* Spath 1935. *a*, Ventral view, ×3; *b*, Right lateral view, ×3; *c*, Same view as in 1*a*, ×1; *d*, Dorsal view, ×1; *e*, Left lateral view, ×1; *f*, Alveolar view, ×1; *g*, Apical view, ×1.

Figs. 2*a*–*h*. BMNH C. 45937. Unfigured paratype II of *R. somaliensis* Spath 1935, No. 253. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view, ×1; *d*, Same view as in 2*a*, ×3; *e*, Same view as in 2*c*, ×3; *f*, Same view as in 2*b*, ×3; *g*, Alveolar view, ×1; *h*, Apical view, ×1.

Figs. 3*a*–*g*. BMNH C. 45936. Unfigured paratype of *R. somaliensis* Spath 1935, No. 251. *a*, Ventral view, ×3; *b*, Right lateral view, ×3. Note the longitudinal lateral ridge which is exceptionally well developed in this specimen; *c*, Same view as in 3*a*, ×1; *d*, Left lateral view, ×1; *e*, Same view as in 3*b*, ×1; *f*, Alveolar view, ×1; *g*, Apical view, ×1.

Figs. 4*a*–*f*. SMC F. 1691 (293). *a*, Ventral view, ×1; *b*, Left lateral view, ×1. Note the well developed longitudinal lateral ridge; *c*, Right lateral view, ×1; *d*, Dorsal view, ×1; *e*, Alveolar view, ×1; *f*, Apical view, ×1.

compressed and somewhat laterally flattened throughout the apical parts of their guards much like those of the slender representatives of the species (Pl. 32, fig. 4*e*). Finally, in a few extreme cases, apparently restricted to extremely sturdy guards with obtusely rounded apical ends, the cross-section of the apical half of the guard is slightly depressed. For example, specimen F. 1687 (Pl. 32, fig. 6*f*) has a depression ratio maximum lateral diameter/maximum dorso-ventral diameter of 9·2/9·0, or about 1·02.

The medioventral groove restricted to the anterior half to three-fifths of the guard in most studied representatives of *Somalibelus somaliensis* (Table 1) is a true ventral canal (Jeletzky 1966, pp. 147, 148) as it is accompanied by an admittedly imperfectly developed splitting surface (see below) and the underlying layers of the guard exhibit distinct to pronounced inward bends throughout its alveolar part (Pl. 30, figs. 1*e*, 2*a*, *b*, 4*c*; Pl. 32, fig. 4*d*). The conotheca is likewise bent inward (Pl. 32, fig. 4*d*) which results in its inner surface forming a sharp longitudinal ridge underneath the medioventral canal.

As pointed out by Spath (1935, p. 223), the strength and length of the medioventral canal varies rather strongly. It is usually restricted to the anterior half (Pl. 30, figs. 3*a*, 5*a*; Pl. 31, fig. 1*a*, *c*) to three-fifths of the guard but may extend over most (Pl. 30, fig. 7*a*, *c*; Pl. 32, figs. 2*a*, *d*, 3*a*, *d*) or even all (Pl. 30, fig. 6*a*, *c*) of its length.

The adoral part of the ventral canal which is mostly limited to the adoral two-fifths to one-half of the guard's length in the most complete specimens, is considerably deeper incised and more narrow than its adapical part. It has a narrowly V-shaped to narrowly U-shaped cross-section. Further adapically the ventral canal rapidly shallows, widens to at least twice its former width and is transformed into a broad, only slightly deepened, poorly delimited furrow. In the majority of specimens studied this furrow rapidly shallows and becomes less and less clearly defined adapically until it disappears completely somewhere before the adapical quarter of the guard. However, in a few aberrant specimens exemplified by specimen F. 13456/21 shown in Pl. 30, fig. 6 this shallow and wide, poorly delimited furrow continues without any weakening right to the apical end of the guard. As noted by Spath (1935, p. 223) the strong development and greater length of the posterior furrow-like part of the ventral canal is characteristic of the more conically shaped representatives of *S. somaliensis*. However, it also occurs in some sturdy specimens (Pl. 30, fig. 1*a*) transitional between the typical form and var. *attenuata* and may be absent in other subconically shaped guards of the species. All extremes are connected by transitions, which indicates a low taxonomic value of the variations in length and strength of the ventral canal on the subspecific, let alone specific, level.

Double lateral furrows were not observed in any of the investigated specimens. Their absence is believed to be an original morphological character of *S. somaliensis* rather than the result of weathering or abrasion, in view of the excellent preservation of the surface of some of the guards (Pl. 31, figs. 3*b*, 4*b*, *c*).

The flanks of all better preserved guards, including the holotypes of the species and *S. s.* var. *attenuata*, are ornamented by single, well-defined to barely perceptible longitudinal ridges (Pl. 30, figs. 1*b*, 5*b*; Pl. 31, figs. 1*b*, *e*, 2*b*, *e*, *f*, 3*b*, *d*, *e*, 4*b*, *c*; Pl. 32, figs. 2*b*, *c*, *e*, 3*b*, *c*, 5*d*, 6*b*, *c*). These 0·8 to 2 mm wide ridges are invariably wider than high, very low in relief (their height is always considerably less than 1 mm), round-topped and poorly delimited from the adjacent parts of the guard's surface. They begin at the oral rim of the guard and extend over the anterior three-quarters to four-fifths of the flanks in all better preserved specimens, gradually weakening adapically and finally fading out before the end of this interval. In no instance were these ridges observed in the immediate proximity of the apex. Their frequent restriction to the oral half of the flanks (Pl. 32, fig. 2*b*, *c*, *e*) appears to be caused by poor preservation of the adapical portions of the guards concerned.

The single longitudinal ridges are situated either in the middle of the flanks or closely adventrally therefrom and are characteristically straight to nearly straight (Pl. 31, fig. 3*b*). However, they may extend slightly obliquely across the flanks, their lower parts gradually shifting adventrally (Pl. 31, fig. 2*e*, *f*) or be gently bent in the middle (Pl. 31, fig. 4*b*). A flattened, or sometimes slightly depressed 2 to 3 mm wide longitudinal zone is commonly situated immediately adventrally of the above described ridges on the adoral half to three-quarters of the guard. This zone gradually narrows and then disappears adapically (Pl. 31, figs. 1*b*, 3*b*, 4*b*; Pl. 32, figs. 3*b*, *c*, 5*d*). It is believed to be the rudiment of the double lateral furrows, especially as it may occasionally (Pl. 32, fig. 2*c*, *e*) be limited by a second longitudinal ridge on the ventral side. Another similarly flattened to slightly depressed longitudinal zone often occurs immediately addorsally of the single longitudinal ridge. Some specimens exhibit only one of these two zones, which may be a matter of preservation only.

The surface of most guards is quite smooth, except for the above described ventro-alveolar canal, longitudinal single ridges, and accompanying flattened to slightly depressed longitudinal zones. However, the well preserved surface of the lower flanks of specimen C-45936 (251) below the apical ends of the longitudinal ridges is locally

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EXPLANATION OF PLATE 32

Somalibelus somaliensis (Spath 1935). Horizon and locality as for Plate 30. V marks the position of the ventral side of the guard.

Fig. 1. SMC F. 1700, polished cross-section, ×4.

Figs. 2*a*–*g*. SMC F. 1708 (355). *a*, Ventral view, ×2; *b*, Right lateral view, ×2; *c*, Left lateral view, ×2; *d*, Same view as in 2*a*, ×1. The apparent extension of the medioventral canal onto the apical half of the guard is an optical illusion (compare fig. 2*a*); *e*, Same view as in 2*c*, ×1; *f*, Alveolar view, ×2; *g*, Apical view, ×2.

Figs. 3*a*–*f*. SMC F. 1709 (350). *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Same view as in 3*b*, ×2; *d*, Same view as in 3*a*, ×2; *e*, Alveolar view, ×2; *f*, Apical view, ×2. Note closely spaced adapical furrows in figs. 3*c*, *d*, and *f*.

Figs. 4*a*–*e*. SMC F. 13456/10. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view, ×1; *d*, Polished cross-section of the alveolar end, ×4. Note the V-shaped inward bending of all layers of the guard and of the white conotheca underneath the medioventral canal. The plane of splitting surface is marked by a light grey weathering; *e*, Apical view, ×1.

Figs. 5*a*–*d*. BMNH C. 42147. Holotype of *Rhopaloteuthis somaliensis* Spath 1935. *a*, Lateral view of the inside of the guard containing most of phragmocone, ×1; *b*, Right lateral view of the outside of the guard, ×1; *c*, Same view as in 5*a*, ×4, to show morphological detail of phragmocone and splitting surface (marked sps) in proximity of alveolar end of the guard and along the ventral surface of the phragmocone. Its contrast with the rough surfaced break on the dorsal and adapical parts of the guard is quite apparent; *d*, Same view as in 5*b*, ×3, to show the presence of a typically developed mediolateral longitudinal ridge.

Figs. 6*a*–*f*. SMC F. 1687. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view, ×1; *d*, Dorsal view, ×1; *e*, Alveolar view, ×1; *f*, Apical view, ×1.

Figs. 7*a*–*f*. SMC F. 13456/11, a halfgrown guard. *a*, Ventral view, ×1; *b*, Left lateral view, ×1; *c*, Right lateral view, ×1; *d*, Dorsal view, ×1; *e*, Alveolar view, ×1; *f*, Apical view, ×1.

covered by faint, ramifying, and irregularly wavering striae. These striae are too feeble to be visible even in the enlarged photographs of this specimen (Pl. 31, fig. 3*b*). Two or three equally faint oblique to subtransversal striae were, furthermore, seen in the proximity of longitudinal depressions and ridges on the flanks of the guard C-45937 (253). There is no assurance that any of these striae are true vascular imprints similar to those observed on the guards of Belemnitellidae; they could be the result of weathering.

The surface of the apex appears to be quite smooth in most of the specimens including all typical representatives of the sturdy variant approaching the holotype and the paratype C-45936 (Pl. 31, fig. 3). However, the apex of some representatives of var. *attenuata* (Pl. 30, fig. 7*a*–*d*, *f*; Pl. 32, fig. 3*a*–*d*, *f*) is ornamented by a variable number of faint to well-marked, short, longitudinal furrows separated from each other by similarly developed longitudinal ridges. These apical furrows and ridges also occur in some guards (Pl. 30, fig. 1*a*–*d*) morphologically transitional between the sturdy variant and var. *attenuata* and possibly in some representatives of the subconical variant (Pl. 30, fig. 6*a*, *c*). The length of these apical furrows and ridges is not known to exceed 4 mm and usually is less than 3 mm. The number of furrows and ridges varies from a few each, restricted to one or both flanks of the apex (Pl. 30, fig. 1*d*) to at least fifteen each (Pl. 32, fig. 3*f*) evenly spaced all around the apex. The medioventral apical furrows and ridges may sometimes be concentrated either exactly adapically of the apical end of medioventral canal (Pl. 31, fig. 7*c*) or inside of its apicalmost part (Pl. 30, fig. 6*c*). No connection between the lateral apical furrows and ridges and the previously described single lateral ridges was observed in any of the investigated guards.

The apex is situated exactly to almost exactly centrally in most of the investigated guards, including all slender specimens characterized by a relatively long and pointed adapical part of the guard. It can, however, be markedly displaced adventrally in some of the sturdy guards characterized by the rounded-subtrapezoidal cross-section of the apical part of the guard (Pl. 30, figs. 2*b*, *c*, *e*, *f*, *h*, 4*b*, *c*, *f*).

Internal morphology. The axial line is subcentral (Pl. 32, fig. 1) to more or less markedly displaced addorsally (Pl. 30, figs. 3*c*, 5*c*; Pl. 32, fig. 5*c*). It is either slightly convex adventrally (Pl. 32, fig. 1) or quite straight throughout its length in sectioned specimens.

The depth of the alveolus fluctuates between about one-half (Pl. 32, fig. 1) and about three-quarters (in paratype II of Spath 1935, p. 223 or C. 45936 of this paper) of the estimated length of the guard (see Table 1) in the most complete specimens studied. It is about 68 % of the estimated length of the guard in the holotype of the species (Pl. 32, fig. 5*a*, *c*). In lateral aspect the ventral side of the alveolus is distinctly concave while its dorsal side is feebly to distinctly convex. The dorso-ventral alveolar angle fluctuates from 23 to 25° in the sectioned specimens (see Pl. 30, figs. 3*c*, 5*d*; Pl. 32, figs. 1, 5*a*, *c*, and Table 1).

The alveolus is pronouncedly to feebly displaced addorsally throughout its length as is clearly visible in all longitudinally split (Pl. 30, figs. 1*c*, *d*, 3*c*, 5*d*; Pl. 32, figs. 1, 5*a*, *c*) and transversely sectioned (Pl. 30, figs. 1*e*, 2*a*, *b*, 4*c*, 5*e*, 6*e*, 7*e*; Pl. 31, figs. 1*f*, 2*g*, 3*f*, 4*e*; Pl. 32, fig. 4*d*) guards. The addorsal displacement of the alveolus is, as a rule, most pronounced at the early and intermediate growth stages and becomes weak to barely perceptible in the latest growth stages of the largest (i.e. adult) guards (e.g. Pl. 31, figs. 2*g*, 3*f*).

Like the cross-sections of the alveolar part of the guard (see in previous section), those of the alveolus are invariably compressed. These cross-sections vary from regularly oval ones with more or less regularly rounded (Pl. 30, figs. 2*b*, 4*c*; Pl. 32, fig. 4*d*) to more or less pronouncedly flattened (Pl. 30, figs. 6*e*, 7*e*) flanks to somewhat egg-shaped ones with the maximum lateral diameter displaced toward the venter (Pl. 30, fig. 1*e*; Pl. 31, fig. 2*g*).

The splitting surface (Jeletzky 1946, pp. 93, 94) of *S. somaliensis* differs from that of all other Belemnopseidae in its perfectly to reasonably smooth part being strongly spatially restricted, and in the rest being more or less level but somewhat to markedly rough-surfaced.

The bottom of the splitting surface begins a few mm adapically of the protoconch and extends subtransversally to the ventral surface of the guard (Pl. 30, fig. 5*d*; Pl. 32, fig. 5*c*). Throughout this interval the almost straight to somewhat adapically convex bottom of the splitting surface deflects slightly adapically forming an angle of about 110 to 120° with the alveolar extension of the guard's axis. The boundary between the somewhat to markedly rough but almost level surface of the splitting surface and the irregularly rugged surface of more adapical parts of the guard is somewhat poorly defined.

An almost to quite smooth area can be distinguished within the above defined splitting surface. It begins either a few mm below the protoconch or approximately at its level. At this level it is restricted to the inner one-quarter to one-third of the space between the ventral surface of the phragmocone and that of the guard. The outer three-quarters to two-thirds of this space are, as already mentioned, rough-surfaced but more or less even.

From its starting-point at or near the protoconch, the boundary between the smooth

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EXPLANATION OF PLATE 33

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa; SMC F. 13456/2. Longitudinal, dorsoventral thin section of well-preserved early part of phragmocone, including protoconch, the first 14 septa, primordial guard, and adjacent parts of conotheca and guard.

Fig. 1*a*. Over-all view of preserved portion of the phragmocone and adjacent guard, ×15.

b. Ventral parts of 7th to 10th septa (marked s) with adjacent parts of conotheca (marked con), and guard (marked g); septal necks of septa 8 to 10 (marked sn) are sharply delimited from adjacent parts of connecting rings (marked cr_9 to cr_{11}); mural parts of all septa torn off the conothecal bulges and displaced adapically. The four-layered structure of the conotheca described in text (see p. 171) is visible, however the thicknesses of individual layers are irregularly changed due to tectonic pressure; individual layers are designated 1 to 4 from the innermost (or first) to outermost (or fourth) inclusive, ×250.

c. Mural end of ventral part of the first septum (marked s) abutting the adapical surface of a triangular bulge of conotheca (marked con); the abrupt contact of the two is clearly visible; septal and conothecal layers obliterated by recrystallization; parts of ventral waist of phragmocone and the adjacent part of proseptum (marked ps) are visible near the lower edge of the photograph, ×750.

d. Ventral parts of 11th and 12th septa (marked s) with adjacent parts of connecting rings (marked cr), conotheca (marked con) and guard (marked g); note the change of orientation of septa as compared with the earlier septa shown in fig. 1*b* and the slit-like appearance of residual ventral parts of camerae (vs), ×250.

e. Ventral parts of 12th and 13th septa with adjacent parts of connecting rings, conotheca and guard; the 13th central camera is even more slit-like than the 12th camera; the same abbreviations as in fig. 1*d*, ×250.

and rough-surfaced parts of the splitting surface extends sub-transversally and adapically convex for a few mm adventrally, and then turns obliquely adorally. Then it runs in a more or less straight line subparallel to the ventral surface of the phragmocone, gradually approaching the ventral surface of the guard to the point 4 to 5 mm below the oral rim of the alveolus. At the latter point (Pl. 30, figs. 3*c*, 5*d*; Pl. 32, fig. 5*c*) the boundary between the smooth and rough-surfaced parts of splitting surface turns abruptly adventrally and extends transversally (often either gently adorally or gently adapically) until it reaches the ventral surface of the guard. This part of the boundary may be either more or less straight or irregularly wavering.

The conotheca is very thin (0·5 mm or less), white, and its surface appears to be almost perfectly smooth to the naked eye. At magnifications ranging from ×2 to ×5 (Pl. 30, fig. 3*c*) its ventrolateral quadrant exhibits very fine subhorizontal striae while its dorso-lateral quadrant exhibits equally fine longitudinal striae (Pl. 30. fig. 5*d*). These striae obviously form part of the characteristic pattern of the conothecal growth lines outlining the early growth stages of the belemnitid proostracum.

Ontogenetic development. The collections studied include no recognizable early juvenile guards and very few half-grown guards. This was probably caused by the bias toward collecting the largest and best preserved specimens on the part of the Arabs from whom these collections were purchased (Spath 1935, p. 227).

The absence of early juvenile guards has forced the writer to rely exclusively on the thin sections for the interpretation of the ontogeny of *S. somaliensis*.

Judging by the limited number of imperfect and often recrystallized thin sections available (Pl. 33, fig. 1*a*; Pl. 35, fig. 1*a*, *c*; Pl. 36, fig. 1*a*, *d*; Pl. 37, fig. 1*a*) the primordial guard of *S. somaliensis* is morphologically intermediate between those of Belemnitidae and Hastitidae on the one hand and other Belemnopseidae on the other, but considerably more similar to representatives of the latter group.

Unlike the relatively slender, cone-shaped earliest growth stage of the primordial guard of *Neohibolites miyakoensis* (Hanai 1953, Pl. VI, figs. 4, 5; Pl. VII, figs. 1–4) and *Hibolithes hastatus* (de Blainville) (Jeletzky 1966, pl. 9, fig. 1A and *unpublished*), that of the primordial guard of *S. somaliensis* is considerably wider, lower, and almost saucer-shaped (Pl. 35, fig. 1*c*; Pl. 36, fig. 1*a*). However, it is considerably larger and thicker than that of Belemnitidae (Jeletzky 1966, pl. 11, fig. 1; pl. 16, fig. 1A) and consists of a greater number (up to 15) of relatively thin, adapically convex, saucer-like transparent calcitic layers separated from each other by thin, more or less opaque brownish grey primordial lines. The deposition of this initial part of the primordial guard (Pl. 35, fig. 1*c*) is followed by the deposition of several much thicker (i.e. longitudinally elongated) broadly and obtusely conical primordial layers (Pl. 36, fig. 1*a*). The change from the saucer-shaped to the conical growth stage is abrupt (Pl. 35, fig. 1*c*). The conically shaped layers become progressively elongated and adapically acute until the cross-section of the primordial guard acquires at first the shape of a very thin and long wedge (Pl. 33, fig. 1*a*; Pl. 37, fig. 1*a*) and then that of a heavy sailor's needle (Pl. 35, fig. 1*a*). This needle-like growth stage of the guard is concluded before the end of deposition of the last layer of primordial guard as its latest layers are thick and abut against the adapical part of the protoconch. Only the immediately following thinly laminated layers of the normal guard (orthorostrum) begin to overlap these latest primordial layers unconformably and to surround the entire protoconch and the adapicalmost parts of the phragmocone proper (Pl. 33, fig. 1*a*; Pl. 37, fig. 1*a*).

No traces of the 'axial tube' (Hanai 1953, pp. 72, 73, Pl. VI, fig. 5; Pl. VII, figs. 2, 4) were observed in the thin sections of *S. somaliensis*. These observations support Jeletzky's (1966, p. 130) conclusion that the 'axial tube' is a mere secondary fracture within one of the primordial guards of *N. miyakoensis*.

The earliest layers of the juvenile growth stage (i.e. of orthorostrum) of *S. somaliensis* retain the above described more or less needle-like shape until they are 8 to 12 mm long. Later these juvenile guards gradually become more and more fusiform (i.e. clavirostrid growth stage in a strict sense). Simultaneously they become less and less slender and generally speaking *Hastites subclavatus*-like (Pl. 32, fig. 1) when reaching the length of 12 to 15 mm. Depending on the degree of further shortening and thickening of these juvenile guards they become either *S. somaliensis* var. *attenuata*-like (Pl. 32, fig. 7) or *S. somaliensis* f. typ.-like (Pl. 32, fig. 4) by the time they are 18 to 22 mm long. The *S. somaliensis* f. typ.-like shape of the guard is not known to change during the remainder of the ontogeny while the *S. somaliensis* var. *attenuata*-like (or any transitional) guard shape may transform itself into a more sturdy adult (i.e. 30 to 33 mm long) shape. This suggests that the above described great variability of the shape of the adult guards of *S. somaliensis* is caused largely by a heterochronous character of the ontogeny of this species. That is, some *S. somaliensis* guards retain the shape characteristic of their early to intermediate growth stages much longer than others (possibly right through the adult growth stages in some instances).

The ontogenetic development of *S. somaliensis* guard differs from that in the Duvaliidae in the insertion of a fairly prolonged and well defined growth stage characterized by a clavirostrid (i.e. fusiform) shape of juvenile guards (Pl. 32, fig. 1) between that of the

EXPLANATION OF PLATE 34

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa; SMC F. 13456/10. Longitudinal, dorsoventral thin section of a fairly well preserved early part of phragmocone, including protoconch, earliest 19 septa, primordial guard, and adjacent parts of conotheca and guard.

Fig. 1*a*. Over-all view of preserved parts of the phragmocone and adjacent guard, ×10.

b. Mural end of the ventral part of 12th septum (marked s) with adjacent parts of 13th connecting ring (marked cr_{13}) and conotheca (marked con); the abrupt contact between the mural part of the septum and the bulge of the conotheca is partly obliterated by recrystallization; the tip of septal neck and the adnation surface (adn) with the 12th connecting ring visible at the lower margin of photograph, ×480.

c. Ventral parts of 7th and 8th septa with adjacent parts of 8th and 9th connecting rings, those of the conotheca and the guard; designations as in Fig. 1*b*, sharp contact between mural part of 8th septum and the bulge of conotheca well preserved and the same is true of the 7th septum visible near the lower margin of the photograph, ×480.

d. Mural part of the 9th dorsal septum with adjacent parts of conotheca and guard showing its well-preserved sharp contact with the bulge of the conotheca; designations as in Fig. 1*b*, ×1000.

e. Mural part of 16th dorsal septum with adjacent parts of conotheca and guard displaying the same morphological details as Fig. 1*d*, ×720.

f. Mural part of the 7th dorsal septum with adjacent parts of conotheca and guard displaying the same morphological details as Fig. 1*d*, ×1000.

g. Mural part of 3rd dorsal septum with adjacent parts of conotheca and guard displaying the same morphological details as Fig. 1*d*, ×1000.

primordial guard on the one hand and that of the short and sturdy, only slightly to feebly subfusiform adult guard on the other. The Duvaliidae are characterized by the persistence of the needle-like guards from the primordial well into the early juvenile growth stage and by the absence or a feeble development of the clavirostrid growth stages.

Microscopic structure of phragmocone and conotheca. Twenty guards or alveolar fragments of *S. somaliensis* have been sectioned to elucidate the microscopic detail of the structure of its phragmocone and conotheca. Only seven usable but fragmentary thin sections and one complete polished plate have been obtained because of the fractured state of most specimens. The thin sections available represent only the earlier parts of the phragmocone. None of them extends beyond the thirtieth septum.

An attempt at a comprehensive reappraisal of the microscopic structure and interpretation of comparative anatomy of the phragmocone and conotheca of the order Belemnitida was recently made by Jeletzky (1966, pp. 110–129). In spite of the somewhat preliminary character of this research, most of Jeletzky's (1966) morphological terms and conclusions have been found to be applicable to *S. somaliensis* and are used unchanged in this paper.

Pls. 33 to 38 inclusive illustrate the most important morphological elements of the phragmocone and conotheca observed in sections of *S. somaliensis*. The following description is essentially restricted to those elements which possess peculiar, taxonomically important features or otherwise add to our understanding of the morphology and comparative anatomy of the belemnitid phragmocone and conotheca. Where the figured morphological elements of *S. somaliensis* phragmocone and conotheca are similar to those of other genera previously described by Jeletzky (1966), the reader is referred to this publication for their complete descriptions.

Conotheca and protoconch. In the best preserved thin sections (Pl. 33, fig. 1*b*; Pl. 35, fig. 2*b*, *c*; Pl. 37, fig. 1*b*, *d*; Pl. 38, fig. 1*c*) the conotheca appears to consist of four well-defined layers which are believed to be homologous to the four layers observed in the conotheca of *Austroteuthis kuehni* by Jeletzky and Zapfe (1967, p. 91, pl. III, fig. 1A, B) and in that of *Megateuthis gigantea* (Schlotheim) by Mutvei (1964, p. 97, fig. 8B).

The best preserved specimens F. 13456/5 (Pl. 35, fig. 2*b*, *c*), F. 13456/1 (Pl. 37, fig. 1*b*, *d*) and F. 1693 (Pl. 38, fig. 1*c*) were studied in ordinary light at magnifications ranging from 250 to 650. The innermost (or first) conothecal layer is of variable thickness, dull brown to bluish grey, transparent to clouded, apparently well calcified and mostly distinctly to strongly and finely laminated throughout. This layer is commonly much darker and more distinctly laminated near its margins than in the middle probably because of the weathering. The innermost layer is very sharply delimited from the mural parts of the septa which discordantly abut against its inner surface. It is less sharply but nevertheless clearly delimited from the second layer of conotheca, except where the two are strongly altered. The innermost layer is about as thick as the second layer between the septa. However, its thickness gradually increases within the conothecal bulges, which consist of this layer alone, until it at least doubles in their middle parts. In the places of its maximum development the innermost layer is two to two and a half times thicker than the second layer and comprises from one-third to about one-half of the total thickness of the conotheca.

The second layer of conotheca is dirty white, cream, or buff coloured, transparent to somewhat clouded and obviously well calcified. It has mostly an almost homogeneous to coarsely and irregularly crystalline appearance in the middle part but may either become replete with vermiform inclusions or show an irregular mesh-like structure elsewhere, especially near the margins. These variations of structure of the second layer appear to be caused by the weathering. The second layer maintains about the same thickness right across the camerae and opposite the mural ends of the septa. Its boundary with the third layer is abrupt and even where the conotheca is best preserved. Elsewhere the two layers may be indistinctly and unevenly delimited (e.g. Pl. 35, fig. 2*c*), which is probably caused by weathering and micro-faulting.

The third conothecal layer is either about as thick as the second or somewhat thinner, where it is best preserved (Pl. 37, fig. 1*d*). It is honey-yellow, light brown, or dark brown

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EXPLANATION OF PLATE 35

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa.

Fig. 1. SMC F. 13456/5. Longitudinal, dorsoventral thin section of well preserved early part of phragmocone including the first 20 septa, protoconch, most of primordial guard and adjacent portions of conotheca and guard.

a. Over-all view of the preserved portion of thin section; pr = protoconch; pg = primordial guard; g = guard proper; siph = siphuncle, ×15.

b. Ventral side of the waist of protoconch and of the first siphonal segment with dorsal and ventral septal necks, ×360. adn = adnation surface; vs_1 = ventral part of first septum; note the apparent continuity of proseptum and conotheca; psv = ventral part of proseptum (grading into conotheca); psd = dorsal part of proseptum; cr_1v = ventral part of first connecting ring; cm = closing membrane (torn off the conotheca on the ventral side); con = conotheca; gi = innermost layers of guard filling out the waist of protoconch; cr_2v = ventral part of second connecting ring; cr_1d = dorsal part of first connecting ring; ds_1 = dorsal part of first septum; cr_2d = dorsal part of second connecting ring; siph = siphuncle.

c. Lower part of protoconch (pr) and the saucer-like earliest part of primordial guard (pg_1) surrounded by the wedge-shaped latter part of primordial guard (pg_2) and the guard proper (g); ×130.

d. Strongly enlarged view of the ventral part of closing membrane, proseptum and the ventral parts of first connecting ring and first septum shown in Fig. 1*b*. adn = adnation surface of first septum and first connecting ring; f = foot of siphuncle; sn_1 = ventral part of first septal neck; other symbols as in Fig. 1*b*; ×650.

Fig. 2. SMC F. 18361 (*a*, *b*). Longitudinal, dorsoventral thin section of well preserved middle portion of the phragmocone and adjacent parts of the conotheca and guard.

a. Over-all view of portion of phragmocone consisting of approximately (estimated) 12th to 24th septa inclusive with adjacent parts of conotheca and guard, ×10.

b. Mural end of dorsal part of 16th septum with adjacent portions of conotheca and guard, ×500. s = septum; con = conotheca; b = bulge of conotheca; ca = Canada balsam exposed in the crack separating conotheca from the mural end of septum; component layers of conotheca marked 1 to 4 inclusive; g = guard.

c. Mural end of the dorsal part of 18th septum with adjacent portions of conotheca and guard, ×500. All symbols the same as in Fig. 2*b*.

d. Dorsal part of 16th septal neck with parts of adjacent connecting rings displaying structural relationships of these elements of phragmocone. s = septum; sn_{16} = septal neck; cr_{16} = 16th connecting ring; cr_{17} = 17th connecting ring; adn = adnation surface of the neck with 16th connecting ring. The gradually tapering adapical part of the 17th connecting ring overlaps the apical end of 16th septal neck and the adoralmost part of the 16th connecting ring. A sharp delimitation of these three elements of phragmocone from each other is quite evident; ×275.

in ordinary light and appears to be less thoroughly calcified than the other conothecal layers. The structure of this somewhat clouded layer varies from relatively coarsely laminated to irregularly meshed and charged with numerous, closely spaced black particles. In black and white photographs, where it is marked by number 3 (Pl. 35, fig. 2*b*, *c*; Pl. 37, fig. 1*d*), the third layer appears to be considerably darker than the adjacent second and fourth layers.

The fourth (or outermost) layer (marked 4 on Pl. 35, fig. 2*b*, *c* and Pl. 37, fig. 1*d*) is mostly similar to the second layer in its colour, structure and inferred degree of calcification. However, it may be dark brown and charged with numerous dark grey to black particles in some specimens (e.g. F. 1693; Pl. 38, fig. 1*c*). The boundary with adjacent dark brown and intensively transversely fibrose innermost layers of the guard is very sharp and discordant (Pl. 38, fig. 1*b*–*d*). The boundary with the adjacent third layer is somewhat hazy.

The specimen F. 13456/1 (Pl. 37, fig. 1*b*, *d*) shows that the above discussed conothecal layers extend into the earliest segments of the phragmocone and at least into the adoralmost parts of the protoconch. The gradual decrease of the conothecal bulges in the earliest two septa appears to be caused by an equally gradual decrease of the swelling of the first conothecal layer within them.

None of the thin-sections permits definitive conclusions about the presence or absence of above described conothecal layers in the lateral and adapical parts of the protoconch's walls. However, specimen F. 13456/3 (Pl. 36, fig. 1*d*) may be interpreted as suggestive of the presence of more than one layer in the adapical part of these walls.

All thin sections studied confirm Jeletzky's (1966, p. 125) reinterpretation of *velamen triplex* of Müller-Stoll (1936). The delimitation of conotheca (c or con.) and the innermost layers of the guard (gi) is especially obvious in the thin section F. 13456/1 reproduced in Pl. 37, fig. 1*b*, *c*, *d*. These photographs show clearly how the poorly layered, spongy-looking innermost layers of the guard (= stratum callosum of Müller-Stoll, 1936, pp. 172–173) are superimposed on the conotheca and fill out the waist of the protoconch. The innermost layers of this 'stratum callosum' appear to pinch out completely adapically on the protoconch's flanks but its outermost layers overlap discordantly the layers of primordial guard (Pl. 37, fig. 1*a*, *b*). The same structural relationships are less distinctly visible in Pl. 35, fig. 1*a*, *b* and Pl. 36, fig. 1*a*, *d*.

Septal layers and their ontogeny. The component layers of septa are indistinguishable in most parts of the thin sections. The mostly crushed and deformed appearance of the septa (Pl. 33, fig. 1*a*; Pl. 35, fig. 2*a*; Pl. 37, fig. 1*a*) and the pronounced changes of their thicknesses within shortest distances (Pl. 37, fig. 1*b*, *c*) suggest that the apparent absence of the component layers is the result of their deformation and concurrent recrystallization. The local presence of remnants of septal layers in better preserved septa (Pl. 36, fig. 1*b*, *c*) confirms this conclusion.

Judging by the preserved remnants of septal layers, the septal structure of *S. somaliensis* and its ontogenetic development were essentially similar to those of other Belemnitida described and figured by Jeletzky (1966).

The specimen F. 13456/1 shows the best preserved layering of the free parts of the earliest twenty septa in spite of their strong deformation and fragmentation (Pl. 37, fig. 1*a*). In this specimen the central layer 'c' extends through about seven-eighths of the ventral parts of the first (Pl. 37, fig. 1*b*, *d*) and the third septa. The more or less homogeneous and transparent layer 'c' comprises at least three-fifths of the thickness of the middle part of these septa. It gradually tapers to nothing shortly before the mural parts and the brims of these septa. The darker coloured upper (n_1) and lower (n_2) outer layers surround the central (c) layer and merge into the undivided outer (n) layer where the central layer (c) pinches out (Pl. 37, fig. 1*d*). No traces of transitional layer 'm' were seen anywhere in these septa. The septal necks of the first and third ventral septa are built exclusively of undivided outer layer 'n'.

The same structural relationships seem to prevail in the less satisfactorily preserved dorsal parts of the earliest few septa of this and some other specimens of *S. somaliensis* (Pl. 33, fig. 1*b*, *c*; Pl. 35, fig. 1*b*, *d*).

The central layer 'c' gradually approaches the brims of the dorsal parts of septal necks in the subsequent septa. It reaches the brims in the 17th to 22nd septa of specimen F. 1693 (Pl. 38, fig. 1*a*, *b*). None of the available thin sections includes any later septa with clearly discernible septal layers.

In the dorsal parts of 17th to 20th septa of the specimen F. 1693 (Pl. 38, fig. 1*a*, *b*) the almost transparent and homogeneous central layer 'c' occupies most of the septal cross-sections and the brownish-yellow, thinly laminated upper (n_1) and lower (n_2) outer layers are restricted to their fringes (Pl. 38, fig. 1*b*). The dark grey and locally black dotted transitional layer 'm' seems to be restricted to small spots at the rounded tips of the central layer 'c'. The whole of the long, slender septal necks, the length of which comprises about one-sixth of that of the corresponding camerae, is built of the undivided outer layer 'n' (Pl. 38, fig. 1*b*).

The above described structure of the dorsal parts of the 17th to 22nd septa of *S. somaliensis* does not differ materially from that of the thirtieth to thirty-first septa of the Belemnitidae s. str. and Cylindroteuthididae (Jeletzky 1966, p. 116, pl. 7, fig. 1B; pl. 8, fig. 2*b*; Pl. 9, fig. 2B). However, it appears to be considerably more advanced than that of the corresponding or even somewhat younger septa of these families (Jeletzky 1966,

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EXPLANATION OF PLATE 36

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa; SMC F. 13456/3. Longitudinal, dorsoventral thin section of well preserved early part of phragmocone, including protoconch, earliest nine septa, primordial guard and adjacent parts of the conotheca and guard.

Fig. 1*a*. Over-all view of preserved portion of phragmocone and adjacent parts of the conotheca and guard; ×40.

b. Mural part of 8th dorsal septum and adjacent parts of conotheca and guard; the septum displays what appears to be a whitish coloured, thin central layer (designated c) flanked by considerably thicker upper and lower transitional zones designated m_1 and m_2, and thin upper and lower outer layers designated n_1 and n_2), ×650 (layer m_2 is designated m_1 in error).

c. Mural ends of 4th and 5th dorsal septa and adjacent parts of conotheca, both septa display what appears to be the same component layers as in the septum shown in Fig. 1*b*. Designations as in Fig. 1*b*, ×650.

d. Protoconch with adjacent parts of the phragmocone and the guard, ×170. The ventral part of proseptum (designated pr.v) appears to merge imperceptibly in the completely recrystallized conotheca. The completely preserved closing membrane (designated cm) appears to be torn off the conotheca on the ventral side. This may be, however, the result of a recrystallization. Dorsal ends of proseptum and closing membrane obscured by nontransparent deposit.

pp. 115–116; Pl. 7, fig. 1E; pl. 9, fig. 2A; pl. 13, fig. 1D). This 'acceleration' of the ontogenetic development of dorsal parts of *S. somaliensis* septa, as compared with those of all hitherto studied Belemnitida is believed to be taxonomically important at least on the generic level, as a similar 'ontogenetic acceleration' was also observed in the adventral migration of the ventral parts of *S. somaliensis* septa.

The apparent presence of similar 'acceleration' in *Hibolithes hastatus* and *Belemnopsis* ex gr. *angusta-apiciconus* (Jeletzky, *unpublished*) suggests that this morphological feature may be characteristic of the family Belemnopseidae as a whole.

Free septum and septal neck of dorsal side. The generally poorly preserved free parts of dorsal septa do not seem to differ materially from those of other Belemnitida described by Jeletzky (1966, pp. 115, 116).

The dorsal parts of the earliest seven to eight septal necks (Pl. 33, fig. 1*a*, *b*; Pl. 35, fig. 1*b*, *d*; Pl. 36, fig. 1*a*, *d*; Pl. 37, fig. 1*a*, *b*) are quite similar to those of *Hibolithes hastatus* (de Blainville) described and figured by Jeletzky (1966, pp. 115, 116; pl. 9, fig. 1A; pl. 10, fig. 1A, B; fig. 7) in their shape, relative length (about one-sixth of the length of corresponding camerae) and structural relationships with the adjacent connecting rings. The first dorsal septal neck is indistinguishable from the subsequent necks in its length and other features (Pl. 35, fig. 1*b*; Pl. 36, fig. 1*d*; Pl. 37, fig. 1*b*). This confirms Jeletzky's (1966, p. 115) conclusion that the dorsal part of the first septal neck of Belemnopseidae is longer than that of Belemnitidae s. str. and about as long as the subsequent septal necks. In *S. somaliensis* the length and other morphological features of dorsal septal necks remain unchanged at least in the earliest twenty-five to thirty septa (Pl. 33, fig. 1*b*; Pl. 35, figs. 1*b*, 2*d*; Pl. 36, fig. 1*a*; Pl. 37, fig. 1*b*; Pl. 38, fig. 1*a*, *b*).

All dorsal septal necks available represent the orthochoanitic growth stage (Jeletzky 1966, pp. 115, 116). No information about the half-grown and adult dorsal septal necks of *S. somaliensis* is available.

The apparent presence of adorally directed prongs in some septal necks of *S. somaliensis* (Pl. 35, fig. 1*b*; see first dorsal neck designated sn_1) appears to be caused by the subsequent plastic deformation of relatively poorly calcified siphonal ends of the septa concerned. These rarely observed adoral prongs are quite irregularly distributed and shaped, occur only in strongly deformed and damaged septa, and alternate irregularly with the prevalent normally developed septal necks.

Free septum and neck of ventral side. Like the dorsal free septa and necks, the ventral free septa and necks of *S. somaliensis* do not seem to differ materially from those of most other Belemnitida (except for Cylindroteuthididae) described by Jeletzky (1966, pp. 117–122).

The ventral parts of septal necks of *S. somaliensis* are invariably longer than their corresponding dorsal parts (Pl. 34, fig. 1*b*, *c*; Pl. 35, fig. 1*b*; Pl. 36, fig. 1*d*; Pl. 37, fig. 1*b*; Pl. 38, fig. 1*b*). Like those of other Belemnitida the ventral parts of septal necks of *S. somaliensis* lengthen, become calcified, and transform from orthochoanitic to suborthochoanitic shape faster than their dorsal counterparts. Furthermore, they become situated adorally of the corresponding dorsal parts of the necks already in the eighth to tenth septum just like those of other Belemnitida (Pl. 33, fig. 1*b*; Pl. 37, fig. 1*a*, *b*; Pl. 38, fig. 1*a*, *b*). Finally, their structural relationships with the adjacent segments of the connecting rings exactly duplicate those described and figured by Jeletzky (1966, pp. 117, 118, figs. 7, 8, 10, 12).

The free parts of the first two to three ventral septa are straight to only slightly convex adapically and form angles from 40 to 50 degrees with the ventral wall of the conotheca. They bend more or less abruptly adapically at the brims so that the septal necks are oriented almost parallel to the ventral wall of the conotheca (Pl. 35, fig. 1*b*, *d*; Pl. 36, fig. 1*a*, *d*; Pl. 37, fig. 1*a*, *b*). The free parts of the next six to seven septa remain virtually straight and more or less abruptly bent at the brims (Pl. 33, fig. 1*b*; Pl. 34, fig. 1*c*). However, they become progressively shorter and shorter and more and more strongly deflected adapically until the angle between the free septum and the conotheca is reduced to only 10 to 12 degrees in the interval from eleventh to fifteenth septa (Pl. 33, fig. 1*b*, *d*; Pl. 34, fig. 1*b*; Pl. 38, fig. 1*c*). This results first in a gradual decrease and then in an almost complete loss of the previously mentioned abrupt bends characteristic of the earliest few septa and in the gradual adventral migration of the successive septal necks. However, these septal necks are somewhat more strongly deflected adapically than the corresponding free septa proper and remain subparallel to the ventral wall of the conotheca throughout this interval. The ventral parts of camerae become correspondingly narrower but retain their trapezoidal shape (Pl. 33, fig. 1*b*, *c*; Pl. 35, fig. 1*b*; Pl. 38, fig. 1*c*) because of the essentially straight (i.e. orthochoanitic) appearance of the ventral necks and connecting rings. The tempo of this ontogenetic change varies considerably from one specimen to another and the thirteenth ventral septum of some specimens (Pl. 33, fig. 1*d*, *e*) may be just as advanced ontogenetically as the fifteenth ventral septum of another (Pl. 38, fig. 1*c*).

EXPLANATION OF PLATE 37

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa; SMC F. 13456/1. Longitudinal, dorsoventral thin section of an early part of phragmocone including exceptionally well preserved proseptum (designated ps), adjacent parts of the conotheca (designated c or con) and the innermost parts of the guard (designated gi); the well preserved primordial guard (designated pg) is partly recrystallized.

Fig. 1*a*. Over-all view of better preserved portion of the phragmocone, primordial guard and guard, ×40.

b. Ventral side of the waist of protoconch, 1st siphonal segment and remains of 2nd siphonal segment with dorsal and ventral septal necks. Proseptum (ps) merges imperceptibly into the conotheca (c) while the latter is sharply delimited from the adjacent innermost layers of the guard (gi) filling the waist of the protoconch. Badly damaged closing membrane is pressed onto the adapical surface of proseptum, ×200.

c. Dorsal side of the waist of protoconch, exhibiting the same morphological features as the ventral side shown in Fig. 1*b*. The junction area of proseptum (ps) and conotheca (con) partly recrystallized and possibly fragmented; the mural parts of otherwise poorly preserved 1st and 2nd septa (s) have a typical appearance and are sharply delimited from the bulges of adjacent parts of conotheca (designated c), ×160.

d. A much enlarged view of best preserved section of the ventral side of the waist of protoconch shown in 1*b*. The four-layered structure of the conotheca described in text (see p. 171) is clearly visible: individual layers are designated 1 to 4 from the innermost (or first) to the outermost (or fourth) inclusive; these layers appear to persist across the waist of the protoconch into the adoralmost part of its wall at least. The structure of the 1st septum (see p. 174) is visible: the central layer (c) is surrounded by the darker coloured upper (n_1) and lower (n_2) outer layers which merge into the undivided layer (n) where the central layer (c) pinches out; other designations as in other figures of this plate, ×450.

The gradual shortening and concurrent increase of adapical deflection of ventral septa continues until the apical ends of the still somewhat more strongly adapically deflected septal necks, and the whole lengths of the sublongitudinally oriented connecting rings, become contiguous with the surface of conotheca in the interval between the thirteenth and seventeenth camerae (Pl. 33, fig. 1*e*; Pl. 38, fig. 1*b–d*). This results in the almost complete disappearance of the adapical three-fifths of the ventral camerae and in their anterior parts becoming narrowly lens-like in cross-section between the conothecal surface and the adapical (now ventral) surface of only slightly addorsally arched septa (Pl. 33, fig. 1*e*; Pl. 38, fig. 1*b*, *d*). The remaining feeble addorsal arching of ventral parts of the septa continues to decrease within the next few camerae until they become almost straight and contiguous with the surface of the conotheca in twentieth and twenty-second camerae. This results in the cross-sections of corresponding residual ventral camerae becoming slit-like, and in their splitting up into two disconnected sections (Pl. 38, fig. 1*d*, *e*). These residual ventral camerae seem to disappear completely in the twenty-third to twenty-fourth camerae but these and subsequent camerae are invariably poorly preserved. The younger ventral septa and necks are not preserved in any of the specimens.

The observed ontogeny of the position, shape, and orientation of the ventral parts of free septa and necks of *S. somaliensis* differs from that of the representatives of the family Belemnitidae s. str. (Jeletzky 1966, pp. 115, 116; pl. 7, fig. 1A, C, D) and Cylindroteuthididae (Jeletzky 1966, pl. 13, fig. 1B, E) in a considerable 'ontogenetic acceleration'. Namely, the apical ends of ventral necks of *Belemnites paxillosus* Lamarck 1801 (Jeletzky 1966, pl. 7, fig. 1A and unfigured) do not become contiguous with the inner surface of conotheca until twenty-sixth or twenty-seventh septum and those of *Megateuthis gigantea* do not become contiguous until thirty-second or thirty-third septum (Jeletzky, *unpublished*). In *Pachyteuthis densa* (Meek 1865) this does not happen until thirtieth to thirty-second septum (Jeletzky, 1966, pl. 13, fig. 1E). In *Gastrobelus umbilicatus* (de Blainville) this does not happen until thirty-fourth or thirty-fifth septum.

The ontogenetic development of ventral necks of *S. somaliensis* is furthermore peculiar in their becoming almost straight and contiguous with the inner surface of the conotheca beginning with the twentieth to twenty-second septa. This is not the case in any of the Belemnitidae s. str. and Cylindroteuthididae studied (Jeletzky 1966, pl. 13, fig. 1B; pl. 15, fig. 1A; fig. 14). In these genera the middle parts of the ventral necks remain more or less strongly arched inward and separated from the inner surface of conotheca by the strongly reduced ventral parts of the camerae at least until maturity (till sixty-fifth septum in *M. gigantea*) and probably throughout their lifetime.

It is not known whether the above described ontogenetic development of ventral parts of free septa and necks of *S. somaliensis* is characteristic of other Belemnopseidae genera. Only the earliest few septa of these genera (e.g. *Hibolithes hastatus*; Jeletzky 1966) have been studied so far.

Mural ends of septa. Jeletzky (1966, pp. 123, 124) experienced considerable difficulties when trying to interpret definitively the structure of mural ends of the septa in the earliest thin sections of *S. somaliensis* phragmocones. The study of additional, better preserved thin sections (Pl. 33, fig. 1*c–e*; Pl. 34, fig. 1*c–g*; Pl. 35, figs. 1*b*, 2*b*, *c*; Pl. 36, fig. 1*b–d*; Pl. 37, fig. 1*c*) indicates that even the mural ends of the earliest septa are completely flangeless. The appreciably thickened, wedge-shaped (in cross-section) mural ends of all better preserved septa of *S. somaliensis* abut the adapical surface of pronounced bulges of the conotheca which are considerably longer than high and somewhat angular in cross-section. The mural ends of ventral septa are very sharply delimited from these conothecal bulges. As already mentioned (see in the section on the conotheca and protoconch) these bulges are built exclusively of the innermost (or first) layer of conotheca, the individual laminae of which can sometimes (e.g. Pl. 35, fig. 2*b*, *c*) be clearly traced within the bulges and directly underneath the contact of the mural ends of septa with the adapical surfaces of the corresponding bulges.

The above observations indicate that the previously suggested (Jeletzky 1966, p. 123) presence of vestigial adoral flanges in the mural ends of the earliest septa of *S. somaliensis* was simulated by their more or less complete recrystallization. This recrystallization resulted in the considerable weakening or complete disappearance of the originally sharp boundary between the septa and conotheca and in the loss of discordant conothecal layers underlying this boundary (e.g. Pl. 34, fig. 1*b*; Pl. 37, fig. 1*d*).

On the dorsal side of the phragmocone the conothecal bulges become more and more prominent in the successive camerae of all thin sections. The same appears to be true

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EXPLANATION OF PLATE 38

Somalibelus somaliensis (Spath 1935) Kimmeridgian (?lower or ?middle), near Bihendula, Somalia, Africa; SMC F. 1693. Longitudinal, dorsoventral thin section of well preserved middle portion of the phragmocone and adjacent parts of the conotheca and the guard.

Fig. 1*a*. Over-all view of portion of phragmocone consisting of 13th to 19th septa inclusive with adjacent parts of conotheca and guard; the adventral part of 20th septum is visible in the left-upper corner of the photograph; ×78.

b. The eighteenth siphonal segment with the ventral part of 17th septum including adjacent parts of conotheca and guard and the dorsal septal necks of 17th and 18th septa. The structure of the dorsal septal necks (see p. 174) is clearly visible, the central layer (c) occupies most of the septal cross-sections, with the upper (n_1) and lower (n_2) outer layers restricted to the fringes; the transitional layer (m) is limited to small spots at the tips of the central layer (c) and the undivided outer layer (n) makes up the entire septal neck; for details of morphology of ventral part of septum see Fig. 1*c*, ×260.

c. Ventral part of 15th septum with adjacent parts of conotheca (con) and guard (g), ×400.

The adapical part of the septum (s) is not yet contiguous with the inner surface of the conotheca (con) but the ventral part of the camera (vc 15) is already slit-like; the ill-defined (?strongly weathered) next adoral connecting ring (cr 16) is separated from the inner surface of the septum by the equally ill-defined (charged with dark grey particles) adapical part of the sixteenth camera (vc 16); the conotheca exhibits the usual four layers numbered 1 to 4 from the innermost to outermost respectively; mural part of the septum strongly altered.

d. Ventral part of 18th septum with adjacent parts of the conotheca and guard, ×400; the adapical part of septum (i.e. septal neck; designated sn 18) is already contiguous with the surface of conotheca leaving only a residual ventral part of the camera (rvc) further adorally; other designations as in Fig. 1*c*; conotheca is recrystallized and does not show component layers.

e. Ventral part of 20th septum with adjacent parts of conotheca and guard, ×400. The septum (s_{20}) is almost straightened with hardly any residual ventral camera (rvc) left between its outer surface and the adjacent part of inner surface of conotheca (con); this remnant of the camera is much smaller than the adjoining adapical remnant of the 21st ventral camera left between the inner surface of the septum and the apical part of next adoral connecting ring (cr_{21}) overlapping the latter; conotheca is completely recrystallized and does not exhibit any component layers but is sharply delimited from the adjacent innermost layers of the guard (g).

of the conothecal bulges of the ventral side where the bulges are less prominent than their equivalents on the dorsal side (compare Pl. 33, fig. 1*b*–*e* and Pl. 34, fig. 1*b*–*c* with Pl. 34, fig. 1*d*–*g*).

The above observations concerning the flangeless character of the mural ends of *S. somaliensis* septa are taxonomically important.

A recent study of earliest septa of *Neohibolites ewaldi* (Jeletzky, *unpublished*) revealed their being completely flangeless and essentially similar to those of *S. somaliensis*. This suggests, in turn, that the somewhat unsatisfactorily preserved mural part of the septum of *N. miyakoensis* Hanai (1953, pl. VI, fig. 1) is likewise flangeless and morphologically similar to those of *N. ewaldi* Strombeck and *S. somaliensis*. The previously suggested presence of the Belemnitidae-like adoral flanges in the mural parts of *N. miyakoensis* septa (Jeletzky 1966, p. 123) is probably erroneous.

The more recent restudy of the somewhat poorly preserved mural ends of the septa of *Hibolithes hastatus* (de Blainville) previously described and figured by Jeletzky (1966, pl. 9, fig. 1A, B; pl. 10, fig. 1A, C) suggests their reinterpretation along the above mentioned lines. These mural ends of the ventral septa may well be completely flangeless and only apparently continuous with the prominent bulges of the conotheca because of weathering and recrystallization of the specimen concerned. It seems possible that the complete absence of adoral flanges of mural parts of septa is diagnostic of all Belemnopseidae.

Proseptum and foot of the siphuncle. Structural relationships observed in thin sections of the specimens F. 13456/5 (Pl. 35, fig. 1*b*, *d*); F. 13456/3 (Pl. 36, fig. 1*d*) and F. 13456/1 (Pl. 37, fig. 1*b*, *c*, *d*) apparently necessitate a revision of Jeletzky's (1966, p. 126) tentative conclusion about a sharp delimitation of the Belemnitida proseptum from the inner layer of conotheca. The well preserved and undamaged ventral part of this proseptum (Pl. 37, fig. 1*b*, *d*) appears to be perfectly continuous with the conotheca and the same seems to be true of the somewhat less satisfactorily preserved and partly fractured dorsal part of this proseptum (Pl. 37, fig. 1*c*). The dorsal part of the satisfactorily preserved proseptum of the specimen F. 13456/3 (Pl. 36, fig. 1*d*) and the apparently undamaged ventral part of the specimen F. 13456/5 (Pl. 35, fig. 1*b*, *d*) also support the idea of a continuity of the proseptum and conotheca. The sharp boundaries observed near the mural ends of some of these prosepta have the appearance of accidental fractures. The same appears to be true of the previously observed (Jeletzky 1966, p. 126) sharp boundaries at the mural ends of other belemnitid genera.

The evidence now available is insufficient for a definitive conclusion. However, it strongly favours the above suggestion concerning the continuity of the proseptum and conotheca in *S. somaliensis* and other Belemnitida. This interpretation is also more sensible because of the following general considerations. Both prosepta of the closely related Ammonitida are known to be the outgrowths of the conotheca in contrast to all their septa proper (Arkell *et al.* 1957, p. L17, fig. 4). Therefore the proposed continuity of the belemnitid proseptum and conotheca strengthens rather than weakens Jeletzky's (1966, p. 126) suggestion that the belemnitid proseptum is homologous with the second ammonitid proseptum while the closing membrane is homologous with the first proseptum and shell caecum of Ammonitida.

The foot of the siphuncle of *S. somaliensis* (Pl. 35, fig. 1*b*, *d*) does not seem to differ significantly from those of other belemnitid genera described by Jeletzky (1966, p. 126, figs. 7, 9, 12, 13).

Connecting ring. No component layers comparable to those recognized by Jeletzky (1966, pp. 127, 128, pl. 7, fig. 1B–E; fig. 6A, B) in the twenty-first to at least forty-fifth connecting rings of other belemnitid genera were recognized in *S. somaliensis*. However, only the earliest twenty-five connecting rings are present in thin sections available. Therefore it is uncertain whether the absence of layering is due to a generally unsatisfactory preservation of all connecting rings studied or to the somewhat delayed development of the component layer in *S. somaliensis* rings.

The structural relationships of all better preserved connecting rings with adjacent septal necks (Pl. 34, fig. 1*b*, *c*; Pl. 35, fig. 1*b*, *d*; Pl. 38, fig. 1*c*–*d*) appear to duplicate those observed by Jeletzky (1966, pp. 126–128) in other Belemnitida.

As the ventral parts of *S. somaliensis* septa become more and more deflected adapically and nearly straightened (see section on the ventral part of free septum and neck), the ventral parts of the next adoral connecting rings approach the adoral surfaces of the septa more and more closely (Pl. 33, fig. 1*b*, *d*, *e*; Pl. 34, fig. 1*b*, *c*). Finally, these rings become almost contiguous with the adoral surfaces of the next adapical septa in the twelfth to fifteenth camerae (Pl. 33, fig. 1*d*; Pl. 38, fig. 1*c*), except for thin to barely perceptible dividing spaces or several lens-like dividing cavities. These structural relationships persist into the youngest well preserved (twentieth to twenty-second; see Pl. 38, fig. 1*a*, *b*, *d*, *e*) ventral parts of the camerae observed. None of the thin sections studied permits a definitive conclusion as to whether or not the still younger connecting rings become completely contiguous with the almost straight ventral parts of their next adapical septa as happens in semiadult and adult (i.e. twenty-fifth to sixty-fifth) septa of all other Belemnitida studied by Jeletzky (1966, pl. 7, fig. 1A, C, D; pl. 11, fig. 2B, C; pl. 13, fig. 1B, E; pl. 15, fig. 1A; pl. 19, fig. 1A, C, F; fig. 10).

Ontogeny of siphuncle and cameral deposits. The distance separating the base of the ventral wall of *S. somaliensis* siphuncle from the ventral surface of the conotheca in the first camera fluctuates between one-quarter of that separating it from the surface of the dorsal wall of the conotheca (Pl. 33, fig. 1*a*; Pl. 34, fig. 1*a*; Pl. 36, fig. 1*a*, *d*) and one-sixth of the latter distance (Pl. 37, fig. 1*a*). The latter figure is believed to be more reliable because of a somewhat better preservation of the protoconch and proseptum in the specimen. The initial position of the siphuncle is, therefore, about the same as that observed by Jeletzky (1966, p. 129) in other Belemnitina and Belemnopseidae. However, it is considerably more adventrally situated than the first segment of siphuncle in *Pseudobelus bipartitus* (Kabanov, 1963, p. 123, fig. 1) and other Duvaliidae (Kabanov 1967, p. 45; figs. 18B, G, V) which was reported to be almost centrally situated.

The general appearance and relative width of *S. somaliensis* siphuncle does not seem to differ materially from those of other Belemnitina and Belemnopseidae studied by Jeletzky (1966, p. 129). The same is true of the gradual adventral migration of *S. somaliensis* siphuncle (Pl. 33, fig. 1*a*; Pl. 34, fig. 1*a*; Pl. 36, fig. 1*a*; Pl. 37, fig. 1*a*).

No traces of cameral deposits were observed in any of the early camerae of *S. somaliensis* (Pl. 35, fig. 1*b*; Pl. 36, fig. 1*a*, *d*; Pl. 37, fig. 1*a*–*d*). This confirms Jeletzky's (1966, pp. 134–135) conclusion about the complete absence of cameral deposits in all Belemnopseidae.

CONCEPT OF SPECIES AND INFRASPECIFIC VARIATION

As clearly recognized by Spath (1935, p. 223), *Somalibelus somaliensis*

> shows great variability and the example figured by Weir seems to have little resemblance to the holotype (Plate XXV, fig. 4). In the latter, and still more so in the paratype II, as in Weir's example, the point is sharp, while in the more elongated var. *attenuata* the shape is still more hastate and the apex long and pointed. There are also specimens (e.g. Nos. 350 and 357) with a more conical shape, and in one of them the ventral groove is unusually long and distinct.
>
> These, however, are all connected with the typical examples by passage-forms (if one can speak of passage-forms when dealing with belemnite guards), and it seems impossible to divide this apparently homogeneous assemblage up into a number of morphological 'species'. Moreover, since they were purchased from the Arabs, and probably were collected at different spots near Bihendula, it would be inadvisable to increase the large number of belemnite species of doubtful horizon.

The writer's restudy of *S. somaliensis* has fully confirmed the above cited conclusions of Spath. All morphologically distinct guards described and figured (Pls. 30–32) in this paper are, therefore, treated as mere morphological variants of a single polytypic *Somalibelus* species. No new formal names were introduced for any of the extreme or intermediate morphological forms of the species.

The grouping of the representatives of *S. somaliensis* according to the outline and proportions of the guard appears to be the best possible solution of the rather intricate problem of organization of numerous distinctive morphological forms included in this species. In distributing the guards among the morphological variants listed in Table 1, it was found necessary, however, to take into account the depth of the alveolus as well as the relative length and distinctiveness of the ventral canal, which show a distinct correlation with the shape and proportions of the guard.

One morphological extreme is represented by the extremely sturdy, relatively less compressed, sybcylindrical guards with obtusely rounded, more or less distinctly mucronated apical end and unusually deep alveolus comprising between three-fifths and three-quarters of the guard's length (Pl. 30, figs. 3, 5; Pl. 31, figs. 3, 4; Pl. 32, figs. 4, 5). This extremely sturdy variant includes the holotype of the species (Spath 1935, pl. XXV, fig. 4; this paper Pl. 32, fig. 5) and so must be treated as its typical variant in spite of its extreme character. Most of the representatives of the extremely sturdy variant are somewhat subclavate in ventral and lateral aspects. This subclavate shape may, however, be stressed or simulated by a commonly present lateral deformation of the alveolar part of the guard (e.g. Pl. 31, fig. 3*a*).

Another extreme variant is represented by much more slender, more or less markedly subfusiform and compressed guards with relatively long and acute apical ends (Pl. 31, fig. 1; Pl. 32, figs. 1, 2, 3). This variant is characterized by the most shallow alveolus which either does not or only slightly exceeds one-half the length of the guard (Pl. 32, fig. 1). The holotype of *S. somaliensis* var. *attenuata* Spath (1935, p. 223; this paper Pl. 31, fig. 1) is a typical representative of this extremely slender variant which also includes more slender and compressed guards with somewhat attenuated adapical quarter (Pl. 32, fig. 3) and much more subfusiform guards (Pl. 32, fig. 2).

The third extreme morphological variant is characterized by slender guards which are feebly to slightly subclavate ventrally and distinctly subconical laterally (Pl. 30, fig. 6). They are strongly compressed throughout, possess an unusually long and distinct medioalveolar canal extending over most or all of the ventral surface and have a characteristically shallow alveolus similar to that of *S. s.* var. *attenuata*. The shape of the apical end varies from the obtuse and distinctly mucronate to the long and acute. This extreme morphological variant is poorly understood, being only represented by about half a dozen fragmentary guards and recognizable fragments.

The extremely sturdy variant of *S. somaliensis* is connected by numerous passage forms with *S. s.* var. *attenuata*. These forms exhibit various combinations of their diagnostic features (e.g. Pl. 30, figs. 1, 7; Pl. 31, fig. 2). Of these morphological forms those combining the more or less long and acute adapical part with the sturdy, more or less subcylindrical shape of the guard and a deep (60–75% of the guard's length) alveolus are the most prominent in the material studied. They are recognized as the fourth morphological variant of *S. somaliensis*.

Other transitional forms combine the slender subcylindrical shape of the guard with a distinctly mucronated apex and long, prominent ventral canal (Pl. 30, fig. 7).

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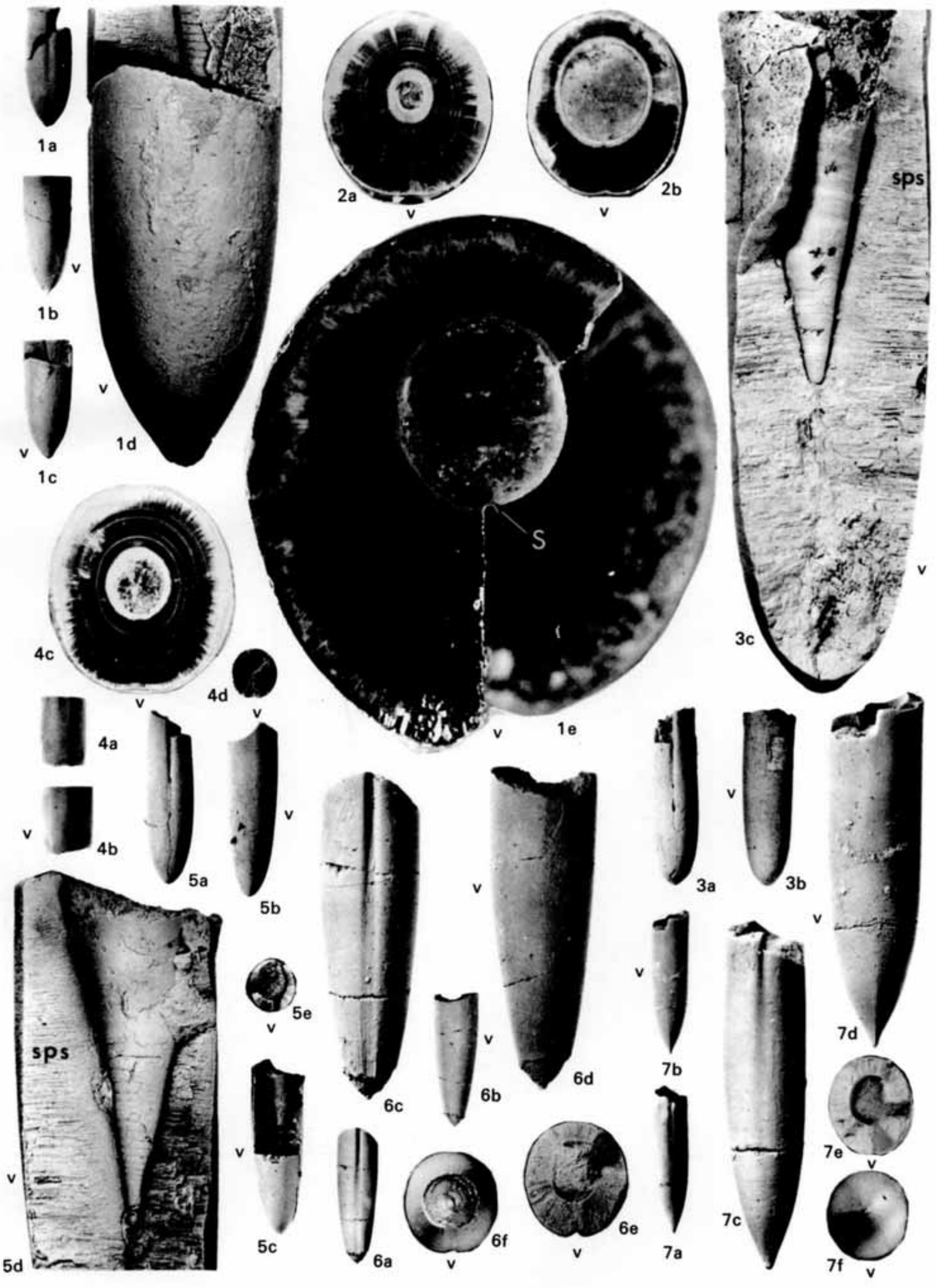
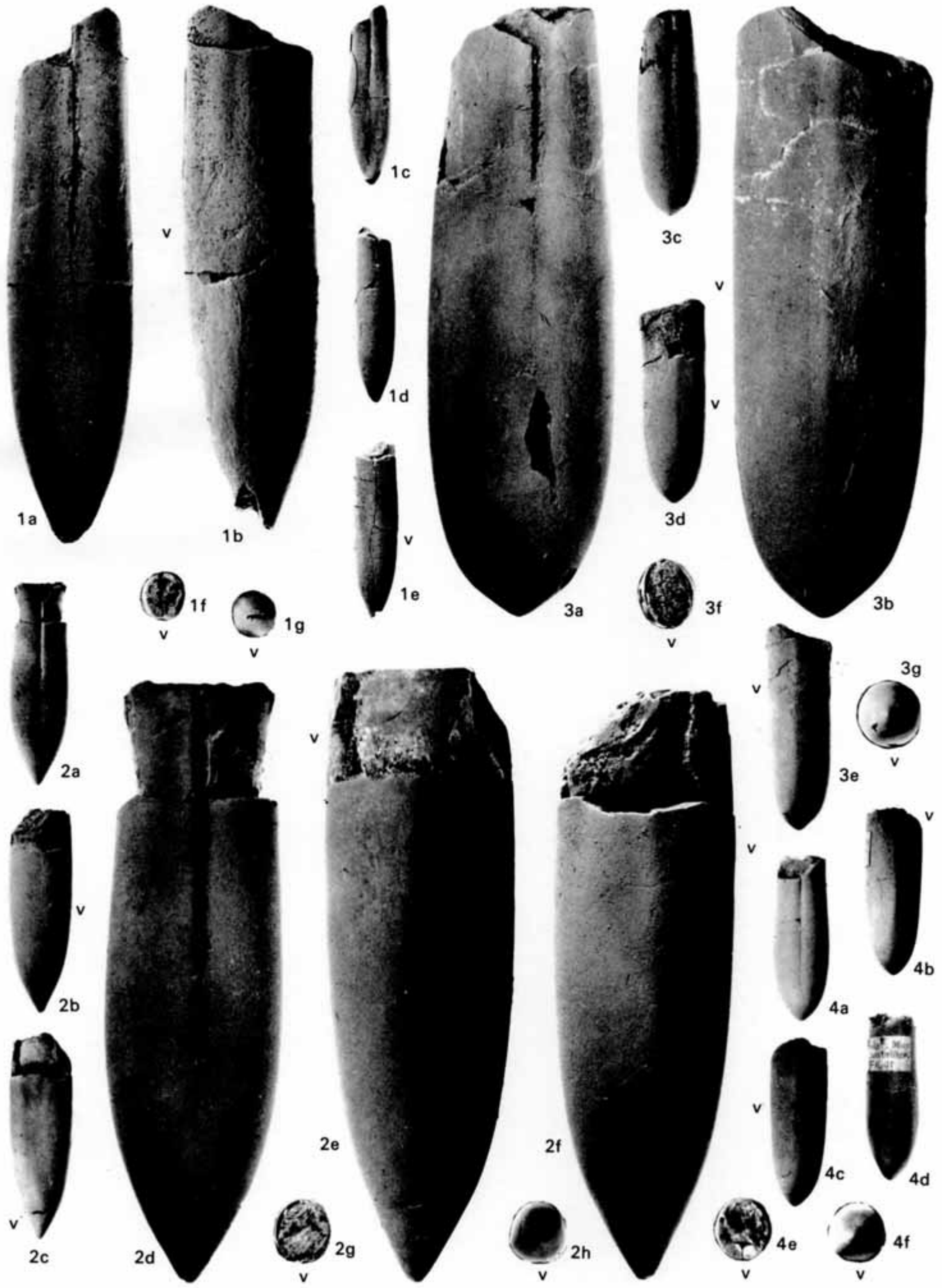


JELETZKY, *Somalibelus somaliensis*



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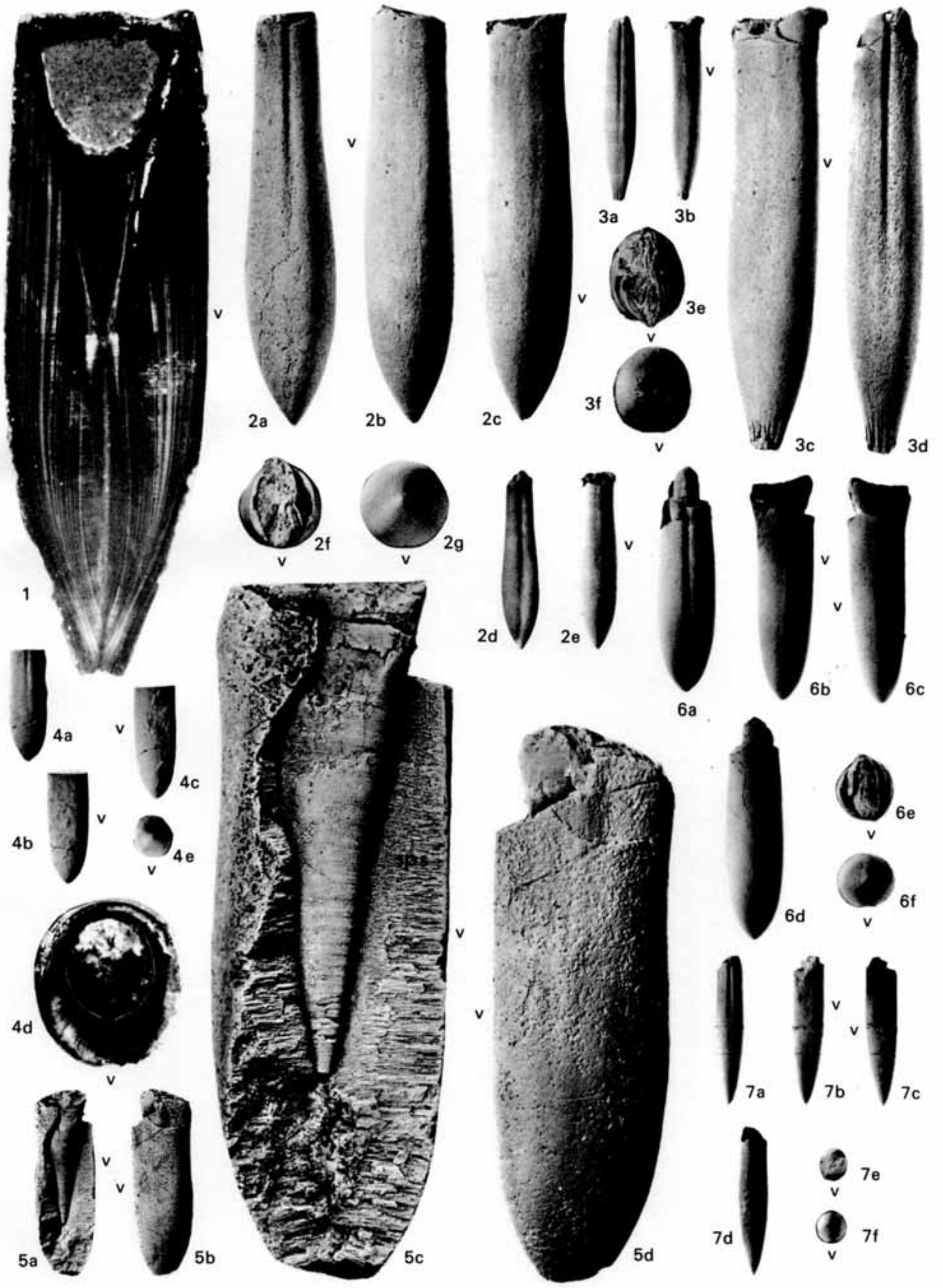

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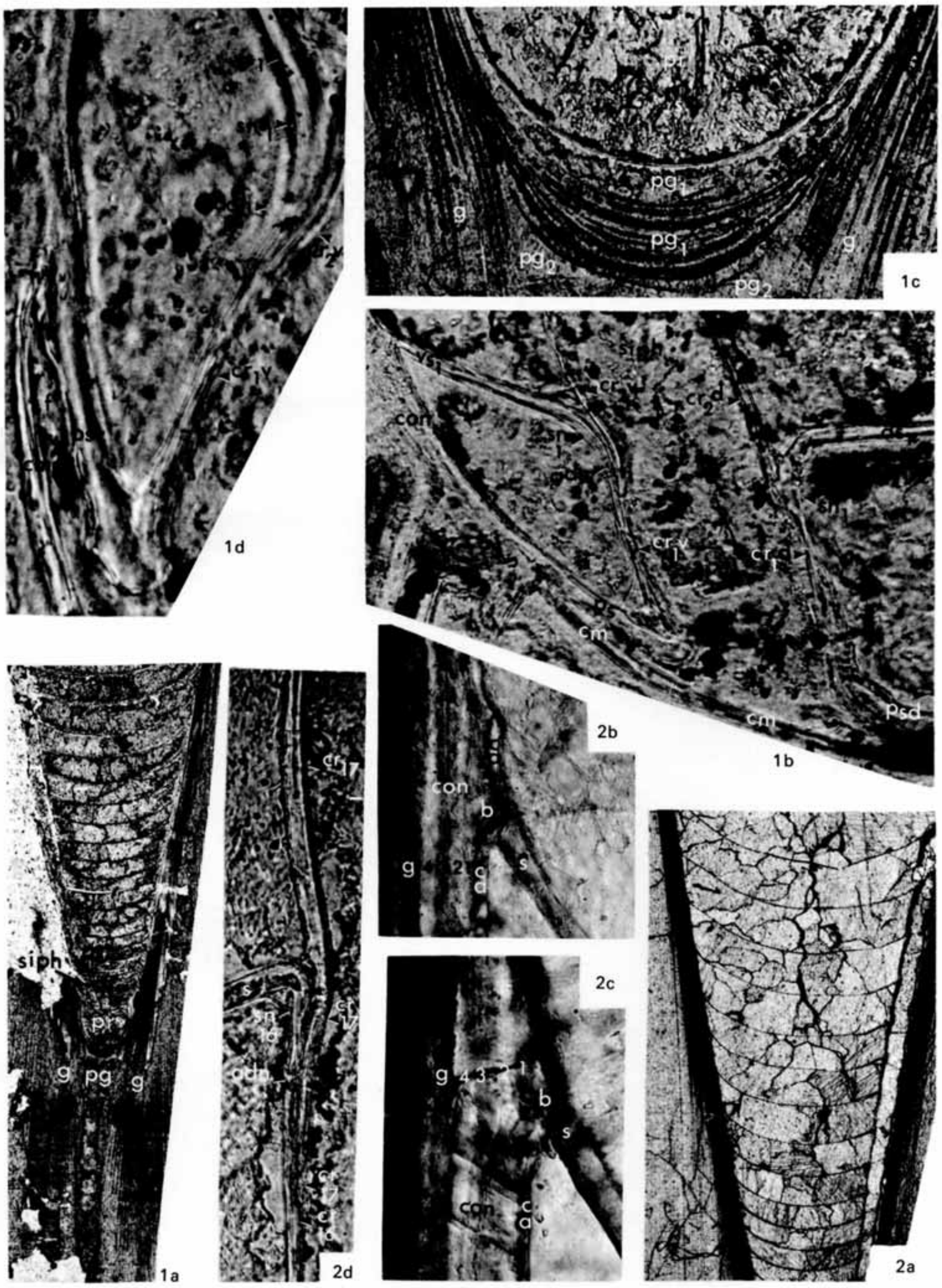
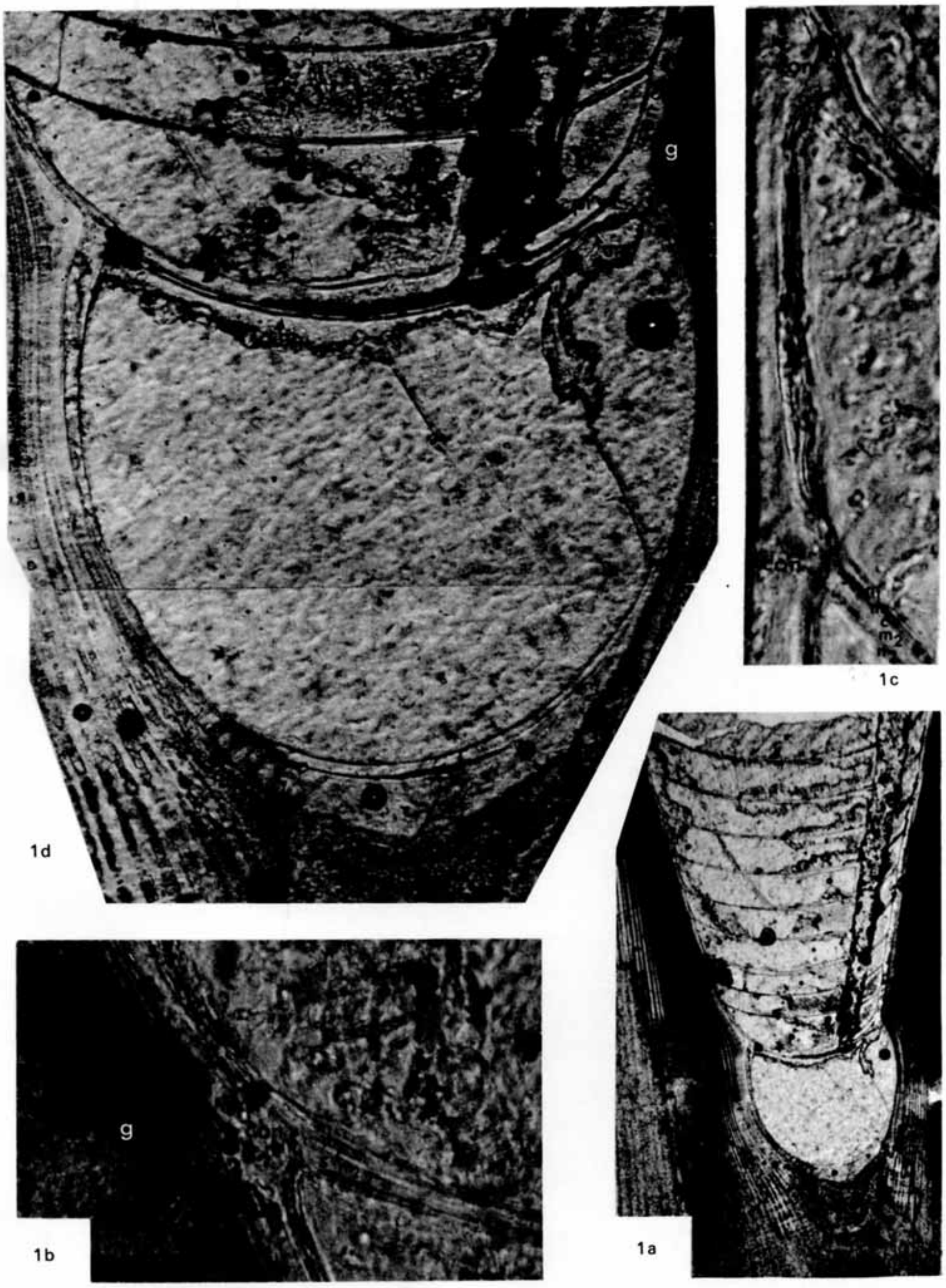


JELETZKY, *Somalibelus somaliensis*

PLATE 36



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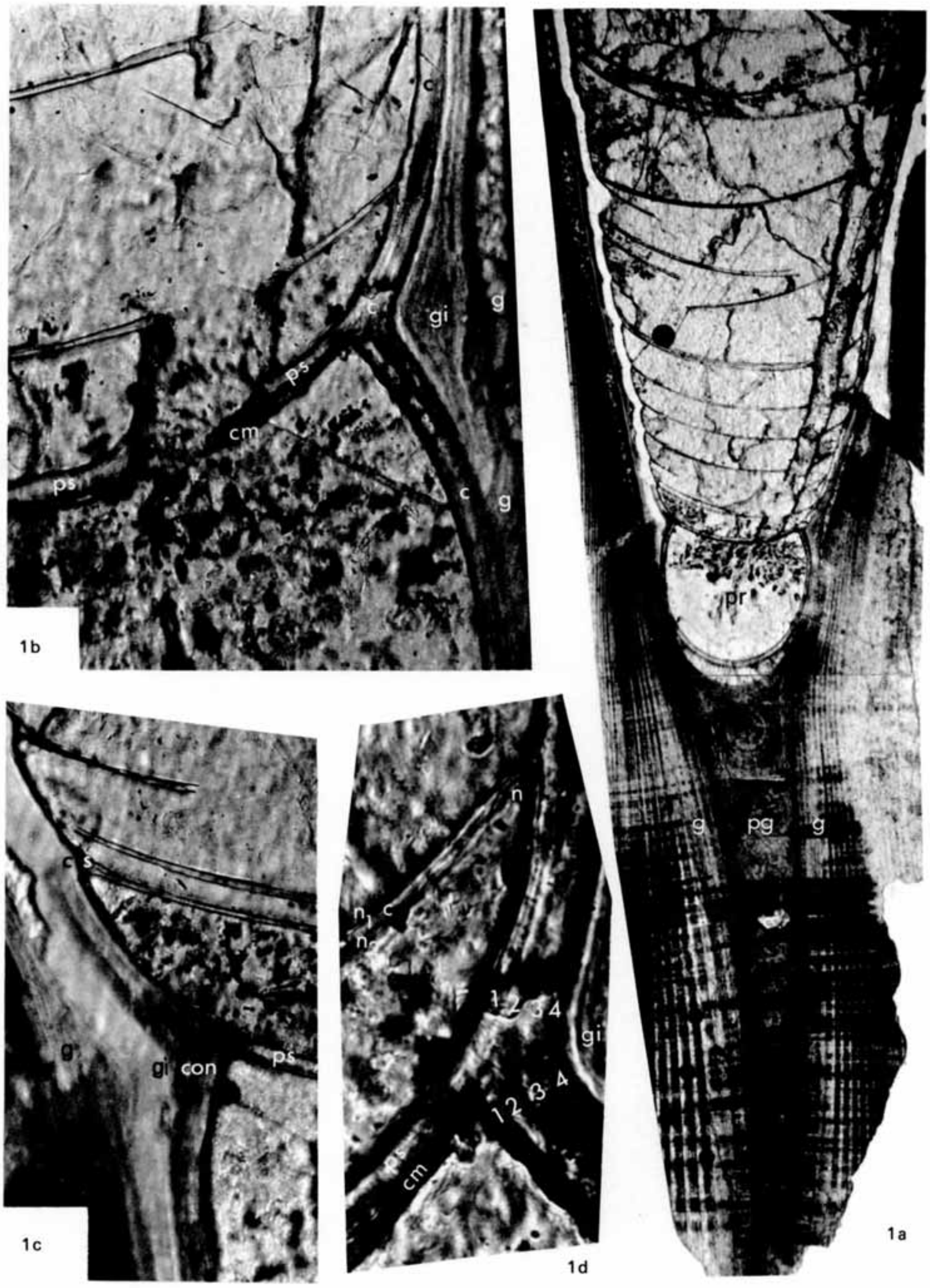

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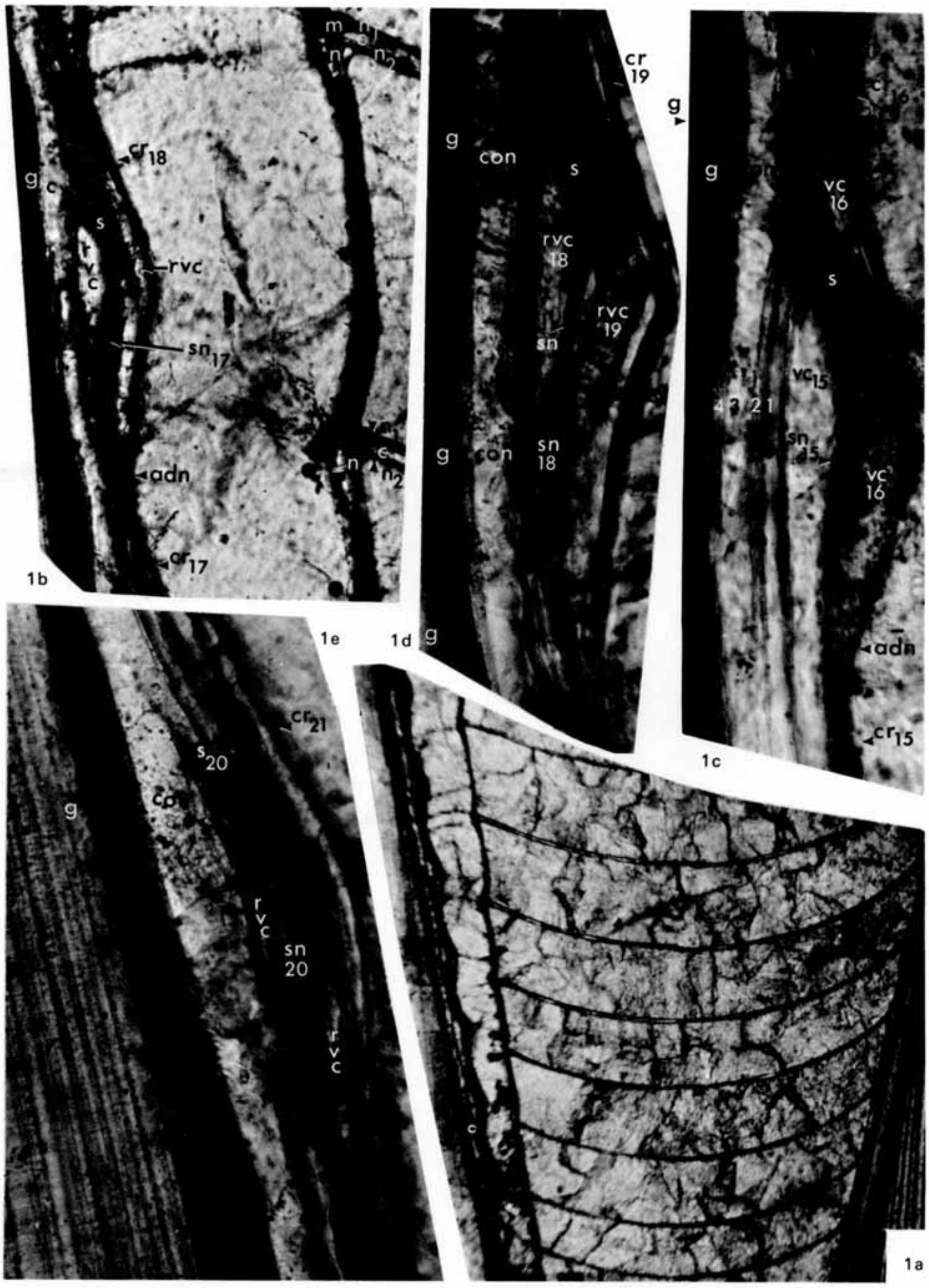

JELETZKY, *Somalibelus somaliensis*

TABLE 1. Critical dimensions and ratios of the best-preserved guards of

Specimens	A *Preserved length*	B *Maximum dorso-ventral diameter (height above apex in brackets)*	*Ratio* B/A	C *Maximum lateral diameter (height above apex in brackets)*	*Ratio* C/A	*Ratio* C/B	*Dors*
Sturdy forms approaching the							
No. 297 (= F. 1694?)	28·1	8·2 (at oral end; appr. guard somewhat crushed)	0·29	8·2 (9)	0·28	1·00	8
F. 1691 (No. 292)	26·5	9·3 (at oral end)	0·35	9·0 (9·1)	0·33	0·97	9
F. 1687 (No. 330)	34·2	9·2 (27·1)	0·26	9·0 (12·5)	0·26	0·97	Dist
C. 45936	32·5	10·2 (17·5)	0·31	10·1 (11·0)	0·31	0·99	Dist
C. 42147 (Holotype of species)	27·5	9·2 (14·0)	0·33	—	—	—	Dist
F. 1690	28·2	8·4 (21·5)	0·29	8·0 (12·3 mm above)	0·21	0·95	Dist
F. 1689 (No. 332)	26·4	8·4 (21·5)	0·32	8·1 (9·2 mm above)	0·31	0·97	Dist
F. 13456/10	17·8	6·9 (10·2)	0·39	6·1 (7·2 mm above)	0·34	0·88	6
Specimens transitional between the sturdy for							
F. 1706	26·2	8·0 (10)	0·31	7·0 (10·6)	0·27	0·88	7
C. 45937	32·0	10·0 (21)	0·31	9·2 (11·0)	0·29	0·92	Brok
F. 1688 (No. 322)	33·1	9·5 (19·5)	0·29	8·6 (12·0)	0·26	0·91	Dist
F. 1705 (No. 335)	25·7	7·4 (12·5)	0·29	7·0 (13·1)	0·27	0·95	Dist
F. 1707 (No. 331)	25·0	7·0 (11·5)	0·28	6·8 (8·0)	0·27	0·97	6
F. 13456/9	19·5	8·0 (at oral end)	0·41	7·8 (9·0)	0·40	0·98	8
Slender forms approaching *Somalibelus soma*							
C. 42146 (Holotype of var. *attenuata* Spath, 1935)	28·0	7·1 (13·0)	0·25	6·5 (12·5)	0·23	0·92	7
F. 13456/11	23·3	5·2 (12·2)	0·22	4·9 (12·2)	0·21	0·94	Dist
F. 1709 (No. 356)	28·5	6·0 (12·2)	0·21	5·2 (9·0)	0·18	0·87	Dist
F. 1708 (No. 355)	27·2	6·0 (10·9)	0·22	6·0 (10·0)	0·22	1·00	Dist
Slender, subcylindrical to s							
F. 13456/15	23·4	6·2 (at oral end)	0·26	5·8 (14·7)	0·25	0·94	6
F. 13456/21	21·4	7·1 (at oral end)	0·33	6·7 (14·5)	0·31	0·94	7

best-preserved guards of *Somalibelus somaliensis* (Spath 1935). All measurements in mm

ameter x in	*Ratio* C/A	*Ratio* C/B	*Diameters at the alveolar end*		*Ratio of alveolar diameters*	*Apical angle (ventral aspect)*	*Alveolar angle (dorsoventral)*	*Preserved depth of alveolus*	*Preserved length of medioventral canal*	*Post-alveola length of guard*
			Dorsoventral	*Lateral*						
Sturdy forms approaching the holotype of the species										
	0·28	1·00	8·2	7·2	0·88	~ 90°	25°	15·7	~ 15·0	12·4
	0·33	0·97	9·3	8·0	0·86	~ 95°	—	—	12·6	—
	0·26	0·97	Distorted	Distorted	—	~ 90°	—	—	21·5	—
	0·31	0·99	Distorted	Distorted	—	~ 120°	—	—	17·5	—
	—	—	Distorted	—	—	—	~ 20–21°	20· 0	—	7·5
above)	0·21	0·95	Distorted	Broken	—	92°	23°	—	14·0	—
bove)	0·31	0·97	Distorted	Distorted	—	~ 90°	—	—	15·2	—
ove)	0·34	0·88	6·6	6·0	0·91	~ 81°	—	—	14·1	—
nsitional between the sturdy form and var. *attenuata* Spath, 1935										
	0·27	0·88	7·6	6·2	0·82	37°	24°	14·1	11·8	12·2
	0·29	0·92	Broken	Broken	—	60°	—	—	16·9	—
	0·26	0·91	Distorted	Distorted	—	~ 72°	—	—	18·5	—
	0·27	0·95	Distorted	Distorted	—	66°	—	—	9·0	—
	0·27	0·97	6·7	5·3	0·79	56°	—	—	16·0	—
	0·40	0·98	8·0	Broken	—	72°	~ 22°	—	10·0	—
approaching *Somalibelus somaliensis* var. *attenuata* (Spath, 1935)										
	0·23	0·92	7·0	6·0	0·86	~ 52°	—	—	12·9	—
	0·21	0·94	Distorted	Distorted	—	36°	—	—	9·0	—
	0·18	0·87	Distorted	Distorted	—	25°	—	—	18·1	—
	0·22	1·00	Distorted	Distorted	—	53°	—	—	13·9	—
Slender, subcylindrical to subconical forms										
	0·25	0·94	6·2	5·5	0·89	~ 45°	—	—	12·1 mm	—
	0·31	0·94	7·1	6·5	0·92	weathered	—	—	19·5 mm	—