

A new Cenomanian (Late Cretaceous) coleoid (Cephalopoda) from Hâdjoula, Lebanon

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Abstract

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Key Words

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soft-tissue preservation

A new vampyropod coleoid from the late Cenomanian limestones of Hâdjoula (north-west Lebanon) is described. *Glyphiteuthis abisaadiorum* n. sp. is classified as a representative of the Trachyteuthididae, mainly on the basis of its general gladius morphology. It represents the fourth species of its genus and the second species of its genus recorded from Hâdjoula. *Glyphiteuthis abisaadiorum* n. sp. differs from *Glyphiteuthis libanotica* in having a more slender gladius. Additionally, the arms are considerably longer in *Glyphiteuthis abisaadiorum* n. sp. than in *Glyphiteuthis libanotica*.

Introduction

The fossil record of cuttlefish, squid and octopus has received relatively little attention. Among malacologists, the opinion is widespread that these mainly soft-bodied coleoids have a poor fossil record. However, thanks to Konservat-Lagerstätten such as the Early Jurassic Posidonian Shales of Holzmaden (Germany), the Middle Jurassic La-Voulte-sur-Rhône (France) and the Late Jurassic Limestones of Solnhofen and Nusplingen, we have a comparatively precise idea about the palaeobiology of Jurassic Coleoidea. For interpretations concerning Cretaceous coleoids, in contrast, we have to rely on the Late Cretaceous Limestones of Hâqel and Hâdjoula (Lebanon), our only evolutionary window into Cretaceous times. Both outcrops are indispensable for morphological studies and phylogenetic reconstructions. It has been recently proven that the contemporary Hâqel and Hâdjoula Limestones not only compete with the Solnhofen Limestones in their state of soft-part preservation, but also in their coleoid diversity (Fuchs 2006a, 2006b, 2007; Fuchs et al. 2009).

In a re-description of trachyteuthid *Glyphiteuthis* (= *Libanoteuthis*) *libanotica* (Fraas, 1878), Fuchs (2006a)

mentioned the possibility that two morphotypes of *Glyphiteuthis* existed in Hâqel and Hâdjoula, but could not prove this observation until additional specimens were available for comparative and quantitative analyses. A collection of coleoids from the Hâqel and Hâdjoula Limestones housed in the Musée National D'Histoire Naturelle in Luxembourg has yielded clear evidence of morphological differences. The aim of this paper is to describe a new species of *Glyphiteuthis* and to distinguish it from *Glyphiteuthis libanotica*.

Geological setting

The examined material comes from the sub-lithographical Limestones of Hâqel and Hâdjoula in north-west Lebanon. These localities are about 15 km apart, 45 km northeast of Beirut and 15 km east of the coastal city of Jbail (Fig. 1). Latest studies confirmed a late Cenomanian age for both Hâqel and Hâdjoula, owing to the presence of the ammonite *Allocrioceras* cf. *annulatum* (Wippich & Lehmann 2004). *Allocrioceras annulatum* is a member of the lower late Cenomanian *Sciponoceras gracile* Zone in the Western Interior of USA and

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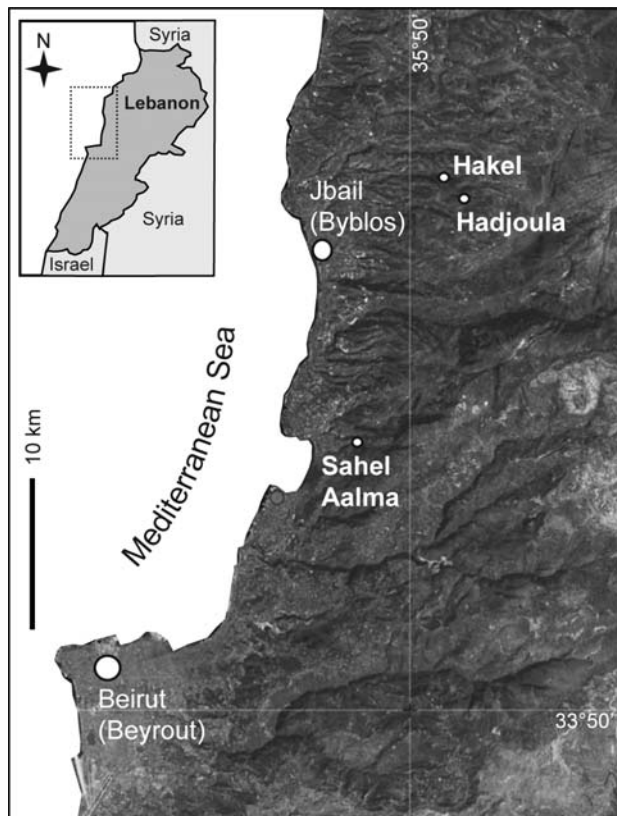


Figure 1. Topographic map of north-western Lebanon showing Hâqel and Hâdjoula in the upper right hand corner (adapted from Fuchs et al. 2009).

the *Metoicoceras geslinianum* Zone of the international standard.

The limestones are hard, fine-grained, well-bedded and laminated: They are often rich in fossils and have a yellowish to greyish colour (Hüchel 1970, 1974; Hemleben 1977; Cappetta 1980).

During the Cenomanian, Lebanon and the whole Arabian Peninsula were part of the African platform in the northern part of the Gondwana super-continent (Philip et al. 1993). In Cenozoic times, opening of the Red Sea separated the Arabian Peninsula from Africa. Like the late Cenomanian Al-Nâmoura outcrops, Hâqel and Hâdjoula were probably deposited in small, shallow Tethyan basins with a reduced water circulation (Dalla Vecchia & Chiappe 2002; Dalla Vecchia et al. 2002). In this scenario, mild oscillations of the relative sea level produced an exceptional sandwich of shallow water carbonate facies (Ferry et al. 2007). The described palaeoenvironment produced favourable conditions for the preservation of a rich fauna, comprising remains of fishes (Forey et al. 2003), reptiles (Dalla Vecchia et al. 2001), crustaceans (Garassino 2000), annelids (Bracchi & Alessandrello 2005), ammonoid and coleoid cephalopods (Wippich & Lehmann 2004; Fuchs 2006a), and others.

Although preservation of coleoid soft-parts is comparatively well-known from Konservat-Lagerstätten, the gladius remains the best-known and therefore systematically most important character complex. The gladius

is a sturdy but flexible chitinous structure within the dorsal mantle of many extinct and living coleoid groups. Terminology and measurements used herein follow those of Fuchs et al. (2007: 577, fig. 1).

Institutional abbreviations. MNHNL, Musée National D'Histoire Naturelle Luxembourg; MSNM, Museo Civico di Storia Naturale di Milano; SMNS, Staatliches Museum für Naturkunde Stuttgart.

Systematic palaeontology

Subclass **Coleoidea** Bather, 1888

Superorder **Vampyropoda** Boletzky, 1992

Order **Octobranchia** Fioroni, 1981

Suborder **Teudopseina** Starobogatov, 1983

Diagnosis. Gladius with clearly reduced and opened conus (spoon-shaped conus). Lateral fields and hyperbolar zones less than half of the gladius length. Hyperbolar zones between lateral and median field as well-developed broad furrows. Anterior median field rounded or pointed.

Families included. Trachyteuthididae Naef, 1921; Teudopseidae Regeteren Altena, 1949; Palaeololiginidae Naef, 1921; Muensterellidae Roger, 1952.

Remarks. The systematic position of the Teudopseina is controversial. The pros and cons for placing teudopseid families within the Vampyropoda are extensively discussed by Fuchs et al. (2007a: 577).

Family **Trachyteuthididae** Naef, 1921

Type genus. *Trachyteuthis* Meyer, 1846; type species *Trachyteuthis ensiformis* Meyer, 1846; Tithonian (Late Jurassic), Solnhofen region, Southern Germany.

Diagnosis. Gladius with granules (tubercles) on the dorsal surface.

Genera included. *Trachyteuthis* Meyer, 1846; *Glyphiteuthis* Reuss, 1854; *Actinosepia* Whiteaves, 1897.

Stratigraphic and geographic range. Middle Jurassic (Callovian) – Late Cretaceous (Maastrichtian); Europe, Central Russia, Lebanon, Cuba, Chile, Antarctica, Australia and North America (see Fuchs et al. (2007a) and Fuchs & Schultze (2007) for more details).

***Glyphiteuthis* Reuss, 1854**

(junior syn. *Libanoteuthis* Kretzoi, 1942)

Type species. *Glyphiteuthis ornata* Reuss, 1854

Diagnosis. Gladius with hyperbolar zone length / gladius length ratio of 0.38–0.39. Anterior median field sharply pointed and with a prominent mid-dorsal keel. Angle of diverging inner asymptotes 30° or less.

Stratigraphic and geographic range. Cenomanian (Lebanon and France), early/middle Turonian (Czech Republic), ?late Santonian (Lebanon).

Species included. *Glyphiteuthis ornata* (= *minor*?) Reuss, 1854 early / middle Turonian Bilá Hora Formation (Czech Republic), *G. libanotica* (Fraas, 1878), *G. abisaadiorum* n. sp., late Cenomanian of Hâqel and Hâdjoula (Lebanon), and *G. boutillieri* (Lennier, 1866) early Cenomanian of Normandy (France).

Remarks. For a long time, “*Geoteuthis*” *libanotica* Fraas, 1878 from the Cenomanian of Hâqel was com-

monly assigned to the genus *Trachyteuthis*. Kretzoi (1942) first recognised differences from *Trachyteuthis hastiformis* and subsequently established a new genus, *Libanoteuthis*. Kretzoi (1942) did not find significant similarities of “*Libanoteuthis*” *libanotica* and *Glyphiteuthis ornata*. Fuchs (2006a) therefore regarded *Libanoteuthis* as a junior synonym of *Glyphiteuthis*.

Glyphiteuthis abisaadiorum n. sp.

Figure 2

2006 *Glyphiteuthis libanotica* Fraas, 1878. – Fuchs: 12, pl. 9, fig. B–C.

Derivation of name. The name is in honour of the family Abi-Saad, the owner of the Hâqel quarry and tenant of the Hâdjoula quarry.

Diagnosis. Gladius slender with hyperbolic zone length/ gladius length ratio of 0.39. Angle of diverging inner asymptotes 23°. Arms at least 1.5 times longer than the gladius.

Holotype. CRE42a + b, deposited in the Musée National D’Histoire Naturelle de Luxembourg.

Paratype. CRE43, deposited in the Musée National D’Histoire Naturelle de Luxembourg.

Type locality. Hâdjoula (34°07′56.70″N; 35°44′41.60″E), Lebanon

Formation and age. *Metoicoceras geslinianum* Zone (international standard; corresponds to *Sciponoceras gracile* Zone in Western Interior); early late Cenomanian.

Description. The holotype, which consists of slab and counter slab, has a preserved length of 230 mm (Figs 2A–C). It shows an extraordinary well-preserved gladius and remnants of mantle musculature, eye capsules, buccal mass, and arm musculature.

On the slab, the gladius is seen in dorsal aspect; on the counter slab as imprints of the external surface of the dorsal side. It is 84 mm in total length and shows only a slight dorsoventral compaction. The posterior half and the most anterior part of the gladius is preserved on the slab. The middle parts are dissolved, but preserved as imprints. Based on distinct growth increments, the gladius can be subdivided into a median field, a pair of comparatively wide and long hyperbolic zones, and a pair of lateral fields (Fig. 2C). The anteriorly sharply pointed median field exhibits an inconspicuous, but distinct mid-dorsal keel as well as very fine granules. The granulated area diverges at an angle of c. 10°. The maximum length of the hyperbolic zone (32 mm) is well-defined through the inner asymptotes. Hyperbolic growth lines are weakly curved. Inner asymptotes open at an angle of 23°; outer asymptotes at 40°. The parabolic lateral fields are 25 mm long. Maximum width of the gladius is 22 mm. Gladius width measured at the anterior end of the hyperbolic zones is 16 mm. After 50% of the total gladius length, the gladius width measures 14 mm.

The mantle outline is easily perceptible owing to preservation of musculature (Fig. 2B). Mantle musculature must be atrophied post-mortem because the mantle length is shorter than the gladius (74 mm). Up to the anterior lateral field end, the gladius tightly fits the entire mantle outline. From this part forwards, the mantle

width is larger than the gladius width. The anterior mantle margin is 28 mm wide. A pair of oval reddish-brown discolorations anterior to the mantle margin can be interpreted as eye capsules, i.e. lateral remnants of the cephalic cartilage (Fig. 2A). Each is 16 mm long and 10 mm wide.

White circular remnants of the buccal mass are visible between the eye capsules and the arm bases (Fig. 2A). Beaks are not preserved. Although the arms are incompletely preserved, the counter slab exhibits an arm length of at least 125 mm (Fig. 2A). Only a few millimetres of the anterior arm tips appear to be missing. The ratio arm length/gladius length is therefore larger than 1.47. The number of arms cannot be determined. Either suckers or cirri are visible. Fins are not preserved.

Similar to the holotype, the paratype preserves a slightly compacted gladius (60 mm length; Figs 2D–F). The dorsoventrally embedded gladius clearly displays the roof-shaped anteriorly pointed median field; it is furnished with a prominent keel on its top (Fig. 2F). Characteristic granules are poorly visible. They are most likely eroded. The gladius width is 16 mm at its maximum extension, 10 mm at the anterior end of the hyperbolic zones, and 9 mm half way along the total gladius length. Inner asymptotes diverge at an angle of 23°; the outer asymptotes at 41°. The hyperbolic zones are 20 mm in length; the lateral fields 16 mm.

The ink sac lies beside the gladius indicating that the dead animal was slightly distorted during embedding. Preservation of arms is incomplete, but they are at least 52 mm long.

Additional specimens that can be determined as *G. abisaadiorum* n. sp. are housed in the Museo Civico di Storia naturale Milano. Specimen MSNMi24801 originates from Hâdjoula, whereas specimens MSNMi 20587 and MSNMi12599 come from Hâqel. Although specimen MSNMi24801 (Fig. 2G) is laterally embedded, it can be determined as *G. abisaadiorum* n. sp. on the basis of its obviously long arms.

Comparisons. Granules on the dorsal gladius surface unambiguously identify present specimens as a trachyteuthid gladius (Fuchs et al. 2007a). The genus *Teudopsis* (Fig. 3A), which exhibits a gladius similar to trachyteuthids, lacks this granulation. In general, gladius indices differ only slightly in *Trachyteuthis* and *Glyphiteuthis* (Tab. 1). Particularly width-length ratios have to be interpreted with care owing to the rate and level of compaction.

Trachyteuthis exhibits a rounded or only weakly pointed anterior gladius end whereas *Glyphiteuthis* shows a sharply pointed anterior gladius end (Figs 3B–E). In *Actinosepia*, the anterior gladius end is serrated (Fig. 3F). Furthermore, the median field in *Glyphiteuthis* is distinctly roof-shaped in cross-section with a prominent keel on its top. In contrast, the median field is smoothly curved in *Trachyteuthis* and *Actinosepia*.

Within the genus *Glyphiteuthis*, gladii differ in width (Figs 2, 3C–E, 4A–E, Tab. 1). The gladius width/ gladius length ratio (GW/GL) is smallest in *G. abisaadio-*

rum n. sp., followed by *G. libanotica*. The gladius of *G. ornata* appears to be the widest (in the single specimen of *G. boutillieri*, the gladius is incomplete). Differ-

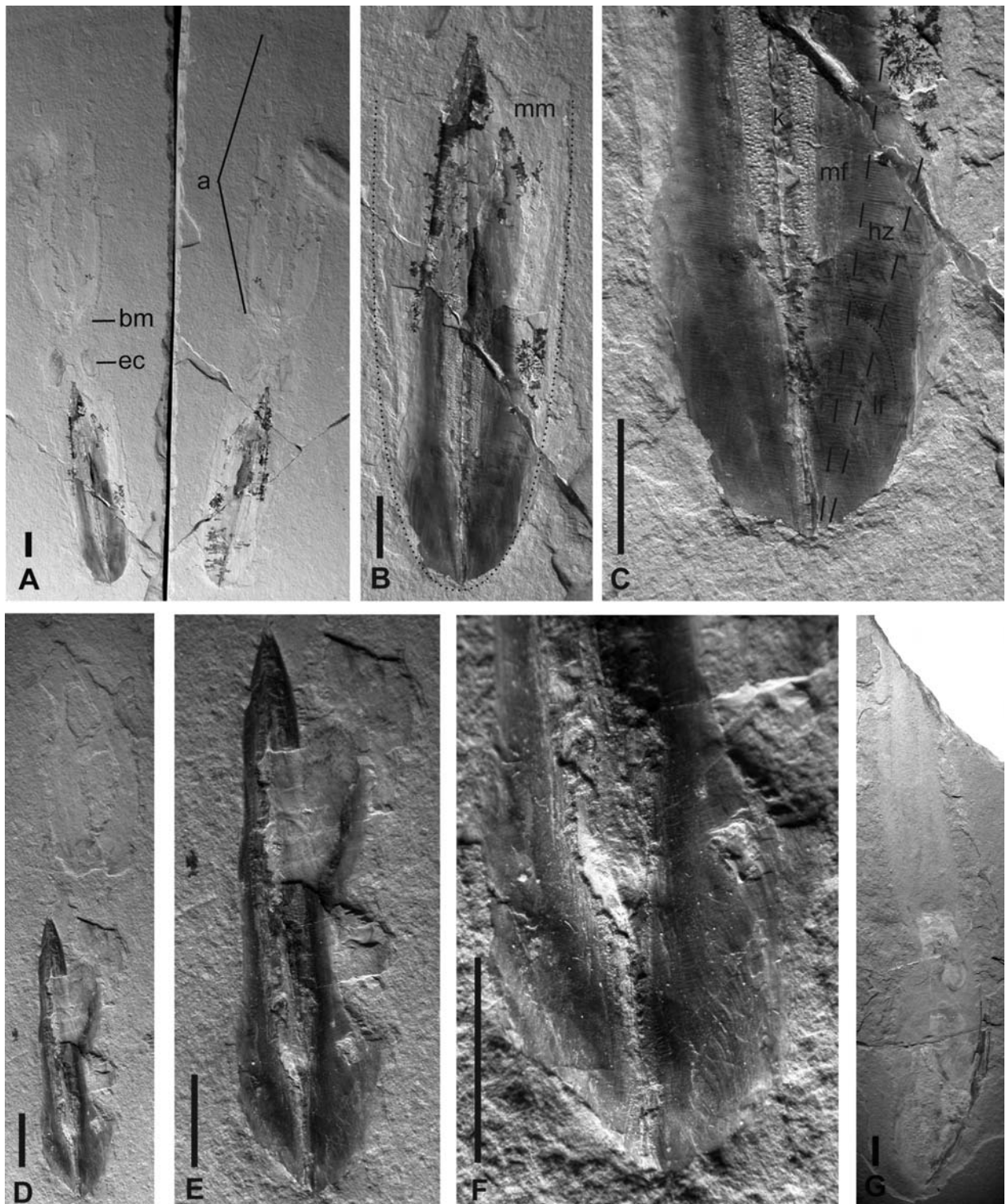


Figure 2. *Glyphiteuthis abisaadiorum* n. sp., from the Upper Cenomanian of Hâdjoula, Lebanon. **A–C.** Holotype (CRE042). **D–F.** Paratype (CRE043). **A.** Slab and counter slab in dorsal view; scale bar = 10 mm. **B.** Close-up of A to show the gladius; scale bar = 10 mm. **C.** Close-up of B to show details of the posterior gladius; scale bar = 10 mm. **D.** Dorsal overview; scale bar = 10 mm. **E.** Close-up of D to show the gladius; scale bar = 10 mm. **F.** Close-up of E to show details of the posterior gladius; scale bar = 10 mm. **G.** Specimen MSNMi24801 seen in lateral view to demonstrate the enormous arm length; scale bar = 10 mm. Abbreviations: **a** – arms; **b** – beak; **bm** – buccal mass; **ec** – eye capsule; **hz** – hyperbolic zone; **ia** – inner asymptote; **lf** – lateral field; **mf** – median field; **mm** – muscular mantle; dashed lines – inner and outer asymptotes.

Table 1. Comparison of morphometric indices and some other gladius characters between *Trachyteuthis*, *Glyphiteuthis abisaadiorum* n. sp., *G. libanotica*, *G. ornata* and *G. boutillieri*.

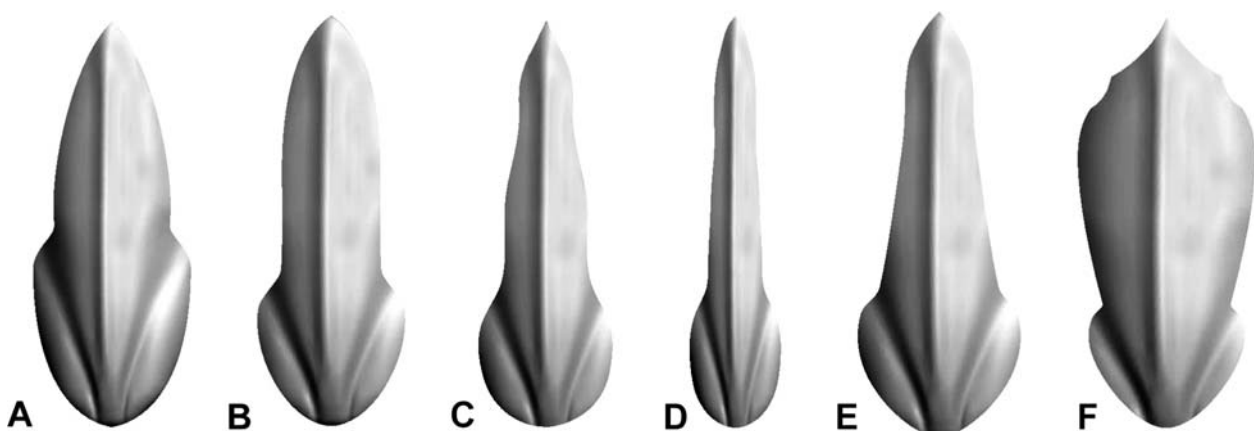
	<i>Trachyteuthis</i>	<i>G. abisaadiorum</i> n. sp.	<i>G. libanotica</i>	<i>G. ornata</i>	<i>G. boutillieri</i>
hyperbolar zone length/ gladius length (HzL/GL)	0.36–0.42	0.38	0.39	0.38	?
lateral field length/ gladius length (LFL/GL)	0.32–0.35	0.30	0.33	0.31	?
gladius width at half way along of gladius length/ gladius length (GW1/2gl/GL)	0.27	0.16	0.20	0.20	?
gladius width at anterior end of hyperbolar zone/ gladius length (GWhz/GL)	0.27	0.19	0.23	0.24	?
maximum gladius width/ gladius length (GWmax/GL)	0.35–0.39	0.26	0.32	0.38	?
angle of diverging inner asymptotes (Aia)	40–43°	23°	28°	30°	?
angle of diverging granulated area (Aga)	large to restricted to keel	c. 10°	c. 17°	c. 8°	?
arm length/gladius length (AL/GL)	/	> 1.47	0.44	?	?
anterior gladius shape	rounded – weakly pointed	sharply pointed	sharply pointed	sharply pointed	sharply pointed

ences in width are additionally expressed by the apical angle (angle of diverging inner asymptotes). Moreover, a slight constriction of the anterior median field present in *G. libanotica* and *G. ornata* is absent in *G. abisaadiorum* n. sp. Finally, *G. abisaadiorum* n. sp. possesses arms that are almost 1.5 times longer than the gladius length. In contrast, arms are considerably shorter than the gladius in *G. libanotica*. In *G. ornata* and *G. boutillieri*, the latter feature is still unknown.

In general, the gladius of *G. abisaadiorum* n. sp. also resembles the palaeololiginid *Rachiteuthis donovani* Fuchs, 2006a from Hâdjoula (rachis-like median field, pointed anterior gladius end, keel). This is only superficial, as *R. donovani* unambiguously lacks the dorsal granulation.

Discussion. Fuchs (2006a: 13) suggested that two morphotypes of *Glyphiteuthis* possibly co-occur in Hâqel. Present observations clearly support this assumption: *G. abisaadiorum* n. sp. is identical with the “slender form” mentioned in Fuchs (2006a) and *G. libanotica* typifies the “stouter form”. Fuchs (2006a) further presumed that arm length is a second character that distinguishes these two forms. The collection of the Musée National D’Histoire Naturelle Luxembourg confirms this observation. The slender gladius of *G. abisaadiorum* n. sp. is associated with arms that are considerably longer than the gladius, while *G. libanotica* is characterised by arms that are shorter than the gladius.

Both *G. abisaadiorum* n. sp. and *G. libanotica* occur in Hâqel and Hâdjoula. *Trachyteuthis* sp. was reported

**Figure 3.** Comparison of gladius shape of teudopseid vampyropods. **A.** *Teudopsis subcostata* (Toarcian). **B.** *Trachyteuthis teudopsiformis* (Tithonian). **C.** *Glyphiteuthis libanotica* (Cenomanian). **D.** *Glyphiteuthis abisaadiorum* n. sp. (Cenomanian). **E.** *Glyphiteuthis ornata* (Turonian). **F.** *Actinosepia canadensis* (Maastrichtian).

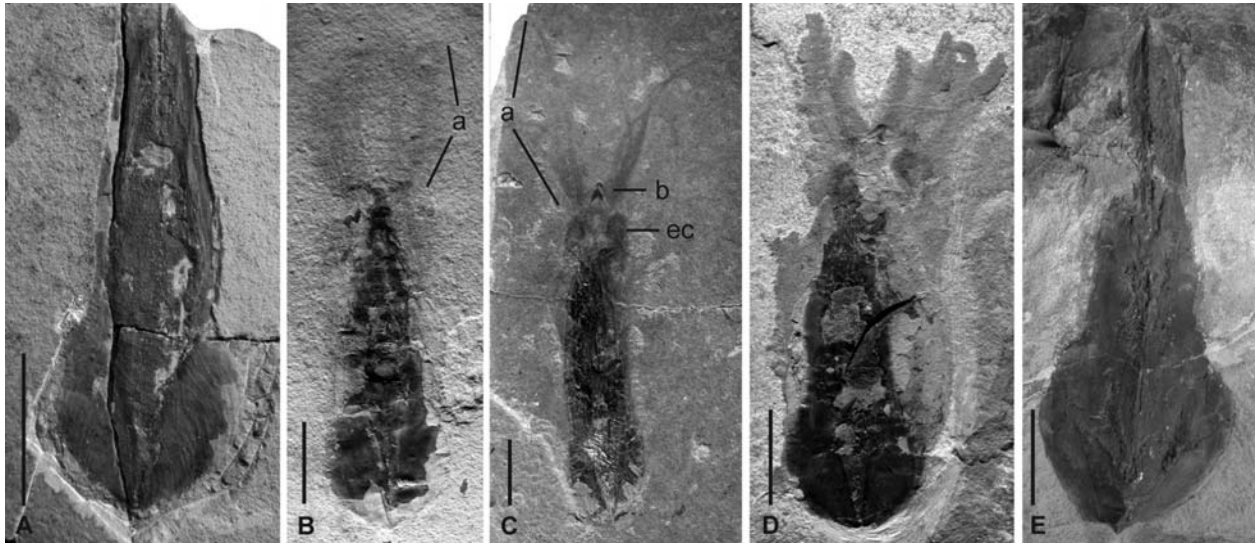


Figure 4. A–D. *Glyphiteuthis libanotica* (Woodward, 1883) from the Upper Cenomanian of Hâqel and Hâdjoula. **A.** Holotype (SMNS 26269) (Hâqel); scale bar = 10 mm. **B.** Specimen CRE041 (Hâqel); scale bar = 10 mm. **C.** Specimen CRE034 (Hâdjoula); scale bar = 10 mm. **D.** Specimen MSNMi25138 (Hâqel); scale bar = 10 mm. **E.** *Glyphiteuthis ornata* Reuss, 1854 (Bohemia); scale bar = 10 mm. Abbreviations as in Figure 2.

from Hâqel, but not from Hâdjoula (Fuchs 2006a). Although Al-Nâmoura is very close to Hâqel and Hâdjoula and considered to be only slightly older, coleoids are still unknown from Al-Nâmoura. The question if this distributional pattern of trachyteuthids is real or a collecting artefact must remain open until new material appears.

So far, *G. abisaadiorum* n. sp. is the most slender member of the trachyteuthids (Figs 3B–F). Fuchs et al. (2007a: 587) regarded *Tr. teudopsiformis* from the Tithonian Solnhofen Limestones to be the connecting link between the Early Jurassic genus *Teudopsis*, the Middle Jurassic–Late Cretaceous genus *Trachyteuthis*, and the Late Cretaceous genus *Glyphiteuthis*. *Tr. teudopsiformis* possesses a mosaic of characters that is shared by *Teudopsis*, *Trachyteuthis*, and *Glyphiteuthis* (e.g. mid-dorsal keel, comparatively narrow granulated area, pointed anterior gladius end). Morphologically and phylogenetically, *Tr. teudopsiformis* is very close to *G. libanotica* and *G. ornata*. *G. abisaadiorum* n. sp. most likely represents a side branch in the trachyteuthid lineage, owing to its slender gladius.

Conclusions

The present study shows that vampyropod coleoids and particularly trachyteuthids were much more diversified than previously thought and that phylogenetically very close taxa co-existed in time and space (Fuchs et al. 2007a, 2007b; Fuchs & Schultze 2007). Superficial similarities between trachyteuthid *Glyphiteuthis abisaadiorum* sp. n. and paleololiginid *Rachiteuthis donovani* further demonstrates a comparatively high amount of convergent developments within coleoid gladii. Gladius morphology is still the most important character to dis-

tinguish vampyropod taxa. The present study also shows that our morphological knowledge is continuously increasing and that soft-tissue characters such as arm length are useful systematic features as well.

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