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PART M, CHAPTER 9C: COMPOSITION AND STRUCTURE OF GLADII IN FOSSIL COLEOIDEA

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Fossil gladii of Jurassic age have the appearance of being mineralized and were thought by Naef (1922, p. 105) to be of original calcareous composition. However, Grandjean (1911, p. 499), in a paper known to Naef, had already recorded that a gladius of *Plesioteuthis* Wagner, 1859, Solnhofen Formation, lower Tithonian, was composed in great part of calcium phosphate, though he carefully added that he had only studied one specimen and did not know whether this was the general case. Later work has shown that it is.

Hewitt (1980) showed that several Mesozoic gladii are composed essentially of the phosphatic mineral francolite, and later work by Hewitt and others (1983) has confirmed this chemical composition. Table 1 demonstrates that phosphatic gladii have been recorded from different facies (see also *Treatise Online,* Chapter 9B). The proostracum of *Phragmoteuthis* Mojsisovics, 1882, from the Sinemurian Charmouth Mudstone Formation, is also composed of francolite (Donovan, 2006).

Francolite is a mineral of the apatite group; it is basically $Ca_5(PO_4)$, in which CO_3, OH, and F may substitute for PO_4 in varying proportions. Francolite is distinguished from dahllite by having more than 1% of F by weight. Its formula has been given as: $Ca_5(PO_4,CO_3)_3(F,OH)$.

ORIGINAL COMPOSITION OF MESOZOIC GLADII

Francolite has been supposed to be the original mineral constituent of Jurassic gladii (Hewitt, Lazell, & Moorhouse, 1983, p. 340). However, phosphate minerals are not known as constituents of extant molluscan shells. Bøggild (1930, p. 236) found molluscan shells to be universally composed of calcium carbonate. The only exceptions he found were the "somewhat doubtful" Torellellidae and Conulariidae, composed of "a phosphoritic substance." Both these families are now excluded from the Mollusca (Fisher, 1962, p. 101, 133).

A second view is that francolite is the product of diagenesis replacing aragonite (A. Seilacher, personal communication, 1981; Hewitt & Jagt, 1999). This raises a difficulty with the Solnhofen fossils, because ammonites, gastropods, and originally aragonitic bivalves are normally found as impressions, aragonite having been dissolved soon after burial (Barthel, Swinburne, & Morris, 1994, p. 100). One would have to assume that francolite replacement in coleoids took place before solution of the aragonite could occur, while for some reason this did not happen with other aragonitic shells. A similar case is the Kimmeridge Clay, Upper Jurassic, Dorset, England, where *Trachyteuthis* Meyer, 1846, gladii preserved as francolite occur on the same bedding plane as ammonites and bivalves, retaining their original aragonitic composition (Hewitt & Wignall, 1988, p. 150).

In fact, modern aragonitic cuttlebones have been experimentally replaced by calcium phosphate using bacterial cultures (Lucas & Prévôt, 1985; Prévôt & Lucas, 1986). However, fossil phosphatic cuttlebones have not been found (Hewitt & Wignall, 1988, p. 149).

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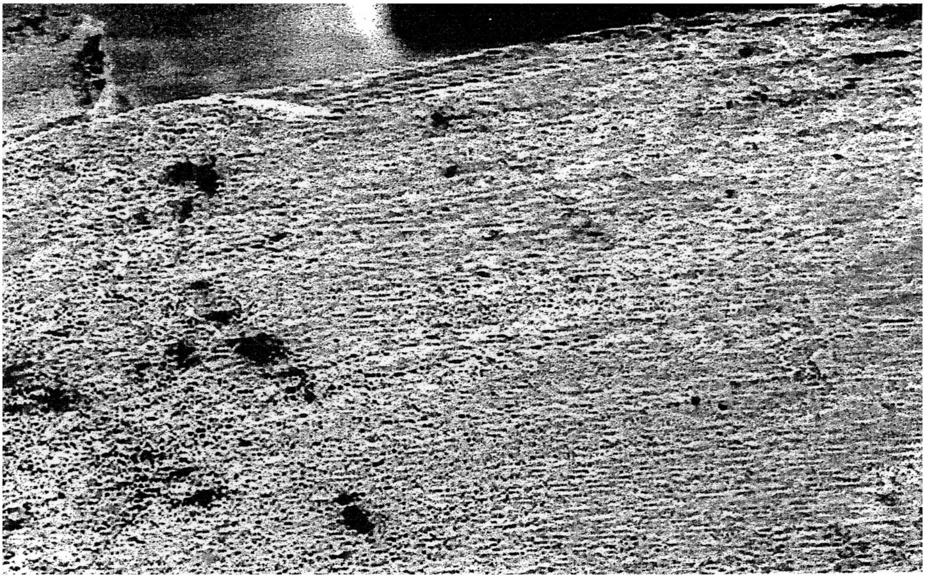
TABLE 1. Fossil gladius composition, phosphatic and francolite (new).

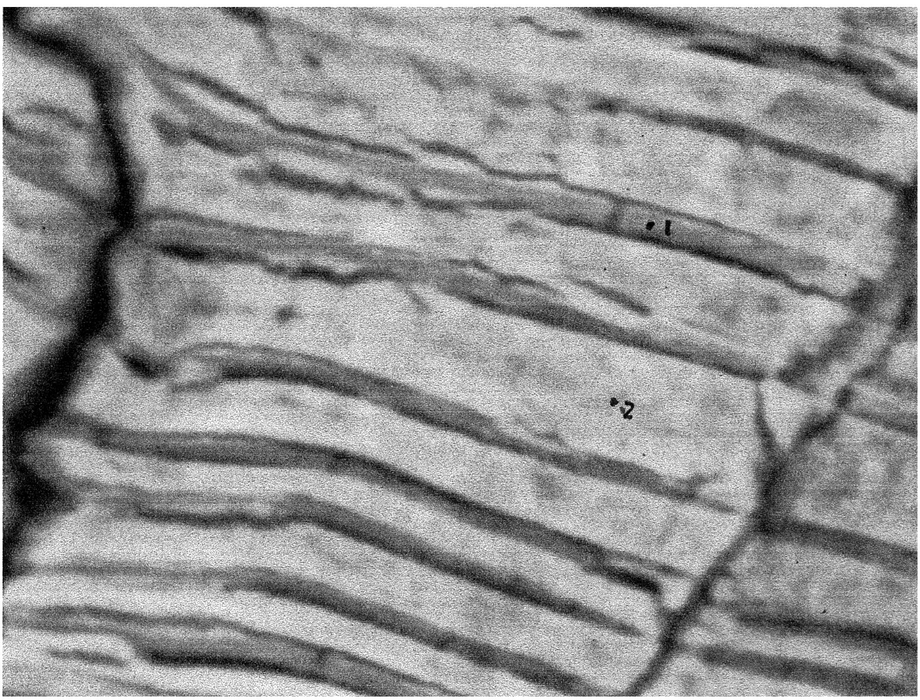
Genus	Origin	Reference	Notes
Loligosepia Quenstedt, 1839	upper Sinemurian, Charmouth Mudstone, UK	Hewitt, 1980, p. 663, 665; Hewitt, Lazell, & Morehouse, 1983, p. 356; Hewitt & Jagt, 1999	"francolite replaced aragonitic and chitinous layers," Hewitt & Jagt, 1999, p. 321
Phragmoteuthis Mojsisovics, 1882	upper Sinemurian, Charmouth Mudstone, UK	Donovan, 2006, p. 681	pro-ostracum
Parabelopeltis Naef, 1921	lower Toarcian, Germany	Hewitt, 1980, p. 663, 665	
Teudopsis Eudes-Deslongchamps, 1835	lower Toarcian	Doguzhaeva & Mutvei, 2003; author observations	
Pearceiteuthis Hewitt & Jagt, 1999	upper Callovian Oxford Clay, UK	Hewitt, Lazell, & Morehouse, 1983; Hewitt & Jagt, 1999	"francolite-replaced layers," Hewitt & Jagt, 1999, p. 319
Plesioteuthis Wagner, 1859	lower Tithonian, lithographic limestones, Germany	Grandjean, 1911; Hewitt, Lazell, & Morehouse, 1983; Wright, Schrader, & Holser, 1987	"phosphate de chaux," Grandjean, 1911, p. 499
Trachyteuthis Meyer, 1846	lower Tithonian, lithographic limestones, Germany	Hewitt, Lazell, & Morehouse, 1983; Wright, Schrader, & Holser, 1987; Hewitt & Wignall, 1988; Hewitt & Jagt, 1999	"selective francolite replacement of the aragonite prism margins," Hewitt & Jagt, 1999, p. 322
Trachyteuthis Meyer, 1846	Tithonian, Antarctic	Doyle, 1991	phosphatic, ?replacing aragonite
Dorateuthis Woodward, 1883	Cenomanian, lithographic limestones, Lebanon	author observations	BMNH C.465
Nesioteuthis Doguzhaeva, 2005	Aptian, siderite concretions, Russia	Doguzhaeva & Mutvei, 2006	"calcium phosphate"
Eoteuthoides Košták, 2002	Turonian, Czech Republic	Košták, 2002	chitin replaced by phosphate
Actinosepia Whiteaves, 1897	Upper Cretaceous, USA	Hewitt & Wignall, 1988; Hewitt & Jagt, 1999	"X-ray diffraction trace ... showed no trace of aragonite," Hewitt & Wignall, 1988, p. 152
Tusoteuthis Logan, 1898	upper Santonian or lower Campanian Smoky Hill Chalk, USA	Hewitt, 1980, p. 661, 663; Hewitt, Lazell, & Morehouse, 1983	
?Niobrarateuthis Miller, 1957	upper Santonian Smoky Hill Chalk, USA	Miller, 1957, p. 809	of "corneous material"

BANDEL and LEICH (1986, p. 142) briefly considered the original composition of gladii from the Solnhofen Formation. They could find no trace of the postulated (NAEF, 1922; JELETZKY, 1966) heavy calcification of the gladius in *Plesioteuthis* and *Leptotheuthis* MEYER, 1834, though they conceded that thin aragonitic calcification could have disappeared during diagenesis.

HEWITT and WIGNALL (1988, p. 153), studying *Trachyteuthis,* concluded that the original shell had a laminar fabric composed of chitinous material, though this did not apply to the tuberculate area on the dorsal surface. DOGUZHAEVA and MUTVEI (2003, p. 884) concluded that gladii of *Loligosepia* QUENSTEDT, 1839, and *Teudopsis* EUDES-DESLONGCHAMPS, 1835, as well as



a



b

FIG. 1. *Teudopsis* sp., Posidonienschiefer, lower Toarcian, Jurassic, Holzmaden area, Baden-Württemberg, Germany, Stuttgart Natural History Museum, no. 64261; transverse sections through gladius and scanning electron micrographs of transverse sections to show the structure; *a,* ×150 (new; courtesy of Jim Davy, Department of Earth Sciences, University College London); *b,* ×1630 (new; courtesy of Andy Beard, Department of Earth Sciences, University College London).

Trachyteuthis, were originally composed of organic matter. This was on the basis of the similarity of ultrastructure to that of extant gladii. DOGUZHAEVA and MUTVEI (2006) concluded that the gladius of the Aptian (Lower Cretaceous) coleoid *Nesisoteuthis* DOGUZHAEVA, 2005, was probably originally chitinous and was converted to phosphate during fossilization.

The balance of probability is that the francolite composing Mesozoic fossil gladii has replaced the original chitin (or chitin-protein mixture, as in extant *Loligo* LAMARCK, 1798).

STRUCTURE

HEWITT (1980, p. 663) found the *Trachyteuthis* shell to consist of laminae 2 µm thick, separated by "porous partings of coarse 0.3 µm diameter francolite." He found similar, but more conspicuously laminated structure, in *Loligosepia* and *Parabelopeltis* NAEF, 1921. Laminated structure was not preserved in *Tusoteuthis* LOGAN, 1898. His section of a *Parabelopeltis* gladius (HEWITT, 1980, fig. 2A) shows laminae up to about 1 µm thick, separated by much thinner layers.

DOGUZHAEVA and MUTVEI (2003, 2006) and FUCHS and IBA (2015) found the gladii of *Loligosepia, Teudopsis,* and *Trachyteuthis* to be composed of laminae similar to the growth increments in extant forms (BIZIKOV, 1996). Each lamina was made up of granules 0.6 to 1.0 µm in diameter and arranged in chains. The granules are the result of diagenesis, but the chains of granules were thought to represent a fibrous structure in the original gladius. In a specimen of *Teudopsis* (Fig. 1*a*), the laminations are clearly visible and are about 6 µm thick, on average. The same specimen under higher magnification (Fig. 1*b*) shows laminae from about 2.5 µm to 9.0 µm thick, alternating with much thinner layers about 1 µm thick. The thin laminae are relatively deficient in francolite and presumably were of different original composition to the alternating thicker layers.

DONOVAN and STRUGNELL (2010) found the gladius of *Palaeololigo* NAEF, 1921, to have been formed by the secretion of additional laminae on the dorsal surface. This also appears to be the case with *Teudopsis.* In extant *Loligo* LAMARCK, 1798, laminae are believed to have been added on the ventral side (HOPKINS & BOLETZKY, 1994), though this was a deduction from the histology of the shell sac, rather than from the structure of the gladius itself.

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