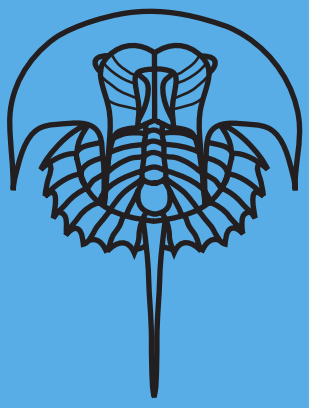

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Systematic Descriptions: Phragmoteuthida

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PART M, CHAPTER 23C: SYSTEMATIC DESCRIPTIONS: PHRAGMOTEUTHIDA

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INTRODUCTION

The Phragmoteuthida Mojsisovics, 1882, is a small and rare belemnoid order that includes one family with two unambiguous genera and four, supposed phragmoteuthid-like forms. It is regarded as being morphologically and phylogenetically transitional between the Paleozoic coleoids (Hematititda Doguzhaeva, Mapes, & Mutvei, 2002; Donovaniconida Doguzhaeva, Mapes, & Mutvei, 2007; Aulacoceratida Stolley, 1919) and the Mesozoic Belemnitida Zittel, 1895. Mojsisovics (1882) first recognized the uniqueness of the family Phragmoteuthidae Mojsisovics, 1882, which Jeletzky (1965) later elevated to ordinal rank. Systematics for this group are shaped by the characteristically wide and three-lobed (tripartite) pro-ostracum, which is significantly different from the spatulate pro-ostracum of the Belemnitida and Diplobelida Jeletzky, 1965 (e.g., Jeletzky, 1966; Donovan, 2006; Doguzhaeva & others, 2007). According to the common idea, a pro-ostracum developed through gradual reduction of the ventral body chamber (see *Treatise Online,* Part M, chapter 8A). The phragmoteuthid type of pro-ostracum encompasses about three-quarters of the phragmocone circumference and, hence, represents an initial state of pro-ostracum formation. The free space of the formerly tubular body chamber has most probably been replaced by muscular mantle, which is supposed to be attached to the lateral margins of the (weakly mineralized) pro-ostracum (Fuchs & others, 2016). The pro-ostracum consists of a central median field with parabolar growth increments and likewise parabolar lateral fields. A narrow area with backwards (hyperbolar) curved or dense longitudinal growth lines—variously called "hyperbolar zone," "arcuated zone," "notch," or "reentrant"—is usually intercalated between the median field and the lateral fields. This tripartite construction is well known from fossil gladii (see *Treatise Online,* Part M, chapter 9B), and it is why many authorities agreed that Mesozoic gladius-bearing coleoids originated within the Phragmoteuthida (e.g., Jeletzky, 1966; Doyle, Donovan, & Nixon, 1994; Donovan, 2006; Fuchs, 2006a, 2006b; Fuchs & Weis, 2008; Schweigert & Fuchs, 2012). For this reason, the Phragmoteuthida appears to be the root of two significantly different evolutionary strategies: one retaining a calcareous phragmocone (Belemnitida) and one entirely losing its buoyancy device through decalcification (Octobrachia Haeckel, 1866). A monophyletical status for the Phragmoteuthida is therefore difficult to establish.

The stratigraphical occurrence of the Phragmoteuthida started with certainty in the Middle Triassic (Anisian) with *Breviconoteuthis* Rieber, 1973. Although the Late Permian *Permoteuthis* Rosenkrantz, 1946, has frequently been regarded as the earliest phragmoteuthid, the single, fragmentary specimen lacks clear evidence of a tripartite pro-ostracum (Jeletzky, 1966). *Permoteuthis* will therefore be treated as a putative phragmoteuthid (Fig. 1). The

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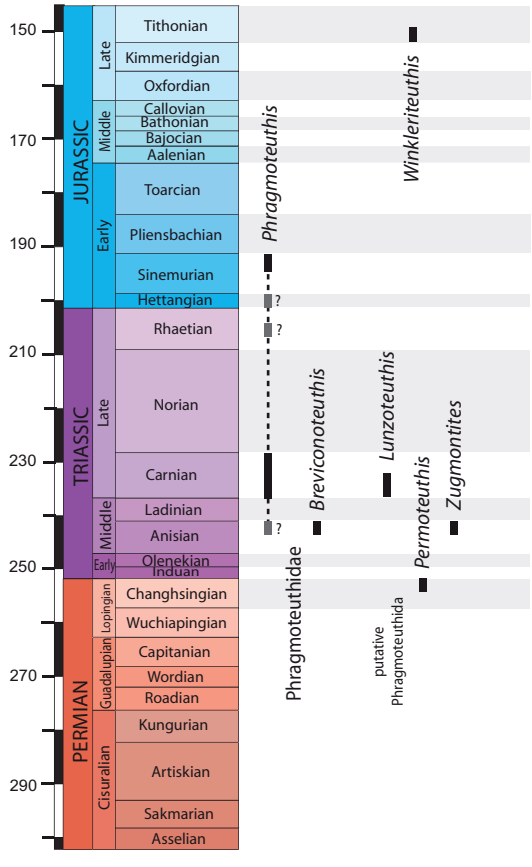

FIG. 1. Stratigraphical occurrences of phragmoteuthid taxa.

Early Jurassic "*Phragmoteuthis*" *montefiorei* (BUCKMAN, 1880) (Callovian) and "*Phragmoteuthis*" *conocauda* (QUENSTEDT, 1849 in 1845–1849) (Toarcian) were known for a long time as the youngest occurrences of phragmoteuthids. However, both species have been reassigned to the (putatively diplobelid) genus *Clarkeiteuthis* FUCHS, DONOVAN, & KEUPP, 2013, owing to the presence of a distinctly narrow proostracum. Therefore, the Sinemurian *Phragmoteuthis huxleyi* from the UK remains the only unambiguous, post-Triassic phragmoteuthid (DONOVAN, 2006). If phragmoteuthid affinities of the Tithonian *Winkleriteuthis* FUCHS, HEYNG, & KEUPP, 2013, are confirmed, the order would have disappeared by the end of the Jurassic.

The assumption of ten-armed Phragmoteuthida was exclusively based on the well-preserved, hook-bearing arm crowns of *Clarkeiteuthis* ("*Phragmoteuthis*") *montefiorei* and *Clarkeiteuthis* ("*Phragmoteuthis*") *conocauda.* The reassignment of the latter species strongly influenced our knowledge: a complete arm crown and, hence, the true number of arms is still unknown from unambiguous phragmoteuthids. The only complete arm crown consisting of ten arms was recorded from a specimen determined as ?*Phragmoteuthis ticinensis* (Anisian, Monte San Giorgio), but it still

lacks confirmation of a tripartite pro-ostracum (RIEBER, 1970).

Order PHRAGMOTEUTHIDA Mojsisovics, 1882

[*nom. transl.* JELETZKY in SWEET, 1964, p. 12, *ex* Phragmoteuthidae MOJSISOVICS, 1882 p. 304; *nom. correct.* JELETZKY, 1965, p. 73, *pro* Phragmoteuthidida JELETZKY in SWEET, 1964, p. 12] [=Phragmoteuthidoidea STAROBOGATOV, 1983, p. 7]

Phragmocone ortho-, brevi-, or slightly cyrtoconic, very small to medium-sized; number of chambers moderate to low, chamber length short; mural parts of septa 30 to 50 percent of chamber length; pro-ostracum weakly mineralized, wide, encompassing three-quarters of phragmocone circumference, three-lobed, subdivided into median field, hyperbolar zones, and lateral fields; lateral fields slightly shorter than median field; protoconch unknown; rostrum aragonitic, investment-like; number of arms uncertain; arm hooks present, possibly biserial, shape variable. *Middle Triassic (upper Anisian)–Lower Jurassic (Sinemurian):* northern Italy, Austria, Switzerland, UK, ?Germany, ?Vietnam.

Family PHRAGMOTEUTHIDAE Mojsisovics, 1882

[Phragmoteuthidae MOJSISOVICS, 1882 p. 304] [=Phragmoteuthidae NAEF, 1921a, p. 534; =Phragmoteuthididae JELETZKY, 1966, p. 37]

Phragmoteuthis MOJSISOVICS, 1882, p. 304 [**Belemnoteuthis bisinuata* BRONN, 1859, p. 44; OD]. Phragmocone medium sized, orthoconic, apical angle 25°–30°; chamber length short; sutures simple; septal necks orthochoanitic, connecting rings extremely long and superimposing 5–6 previous rings; siphuncle marginal; pro-ostracum length equals phragmocone length, anterior median field weakly acute; lateral field slightly shorter than median field, relative length variable; hooks variable, stylet-like or with strongly curved uncinus. *?Middle Triassic (upper Anisian), Upper Triassic (lower Carnian)–Lower Jurassic (upper Sinemurian):* northern Italy, Austria, UK, Switzerland, ?Germany, ?Vietnam.——FIG. 2,*1a–b*. **P. bisinuata* (BRONN), Carnian, Cave de Predil (Raibl), northern Italy; *a,* specimen NHMW 1864/52/47 (original of MOJSISOVICS, 1882, pl. 94,*3*), showing laterally compacted, three-lobed pro-ostracum, ×1.6 (Doguzhaeva & others 2007; photo by H. Summesberger); *b,* specimen showing differentiation of arm hooks, ×2 (new; photo by H. Summesberger).——FIG. 2,*1c–f, P. huxleyi* DONOVAN, upper Sinemurian, Charmouth Mudstone Formation, Dorset, UK; *c,* paratype, BMNH 83963, ventral view, ×0.4 (Donovan, 2006, fig. 4A); *d,* 3-D reconstruction, ventral view (new); *e,* paratype, BMNH 83963, dorsolateral view, ×0.4 (Donovan, 2006, fig. 4B); *f,* 3-D reconstruction, dorsal view (new).

Breviconoteuthis RIEBER, 1973, p. 7 [**Atractites breviconus* REIS, 1907, p. 148; M]. Phragmocone very small to small, brevi- to slightly cyrtoconic, circular in cross section, apical angle 38°–40°; ratio of chamber length to diameter about 0.15; pro-ostracum three-lobed, longer than phragmocone, anterior median field rounded; siphuncle marginal; rostrum unknown. *Middle Triassic (upper Anisian):* Switzerland (Canton Ticino), Austria.——FIG. 2,*2a–b*. **B. breviconus* (REIS), upper Anisian, Grenzbitumenzone, Monte San Giorgio, Switzerland; *a,* specimen PIZ M/21, dorsal view showing three-lobed pro-ostracum, ×1.5; *b,* specimen PIZ M/12, dorsal view showing breviconic phragmocone, ×1.5 (new; originals of Rieber, 1974, fig. 1–4).

PUTATIVE PHRAGMOTEUTHIDA

Lunzoteuthis DOGUZHAEVA, SUMMESBERGER, & MUTVEI, 2006, p. 71 [**L. schindelbergensis*; OD]. Phragmocone very small, breviconic, ratio of chamber length to diameter about 0.33; pro-ostracum with median field and arcuated zones. *Upper Triassic (lower Carnian):* Austria.——FIG. 3,*1*. **L. schindelbergensis,* lower Carnian, Schindelberg, Lunz, Austria, holotype, NHMW2005z0005/1, showing dorsal fragments of phragmocone with anteriorly projecting growth lirae of the median field (*cf*), ×7 (Doguzhaeva, Summesberger, & Mutvei, 2006, pl. 1A).

Permoteuthis ROSENKRANTZ, 1946, p. 161 [**P. groenlandica;* M]. Known only from a small piece of shell that appears to represent a fragment of a three-lobed pro-ostracum. [The name *Permoteuthis* was applied by ROSENKRANTZ (1946) to several fossils that may or may not belong to the same species. It was restricted by JELETZKY (1966, p. 38) by designation of the pro-ostracum fragment.] *Upper Permian (Changhsingian):* eastern Greenland.——FIG. 3,*2*. **P. groenlandica;* line drawing of a putative, fragmentary pro-ostracum, ×0.5 (new).

Winkleriteuthis FUCHS, HEYNG, & KEUPP, 2013, p. 242 [**Acanthoteuthis problematica* NAEF, 1922, p. 183; OD]. Phragmocone small, breviconic, otherwise poorly known; lateral fields of the pro-ostracum well developed and anteriorly (parabolar) projected; onychites uniform, biserial, base short, shaft slightly inclined, uncinus weakly curved. *Upper Jurassic (lower Tithonian):* southern Germany.——FIG. 3,*3a–e*. **W. problematica* (NAEF), lower Tithonian, Solnhofen Formation, Eichstätt region, Germany;

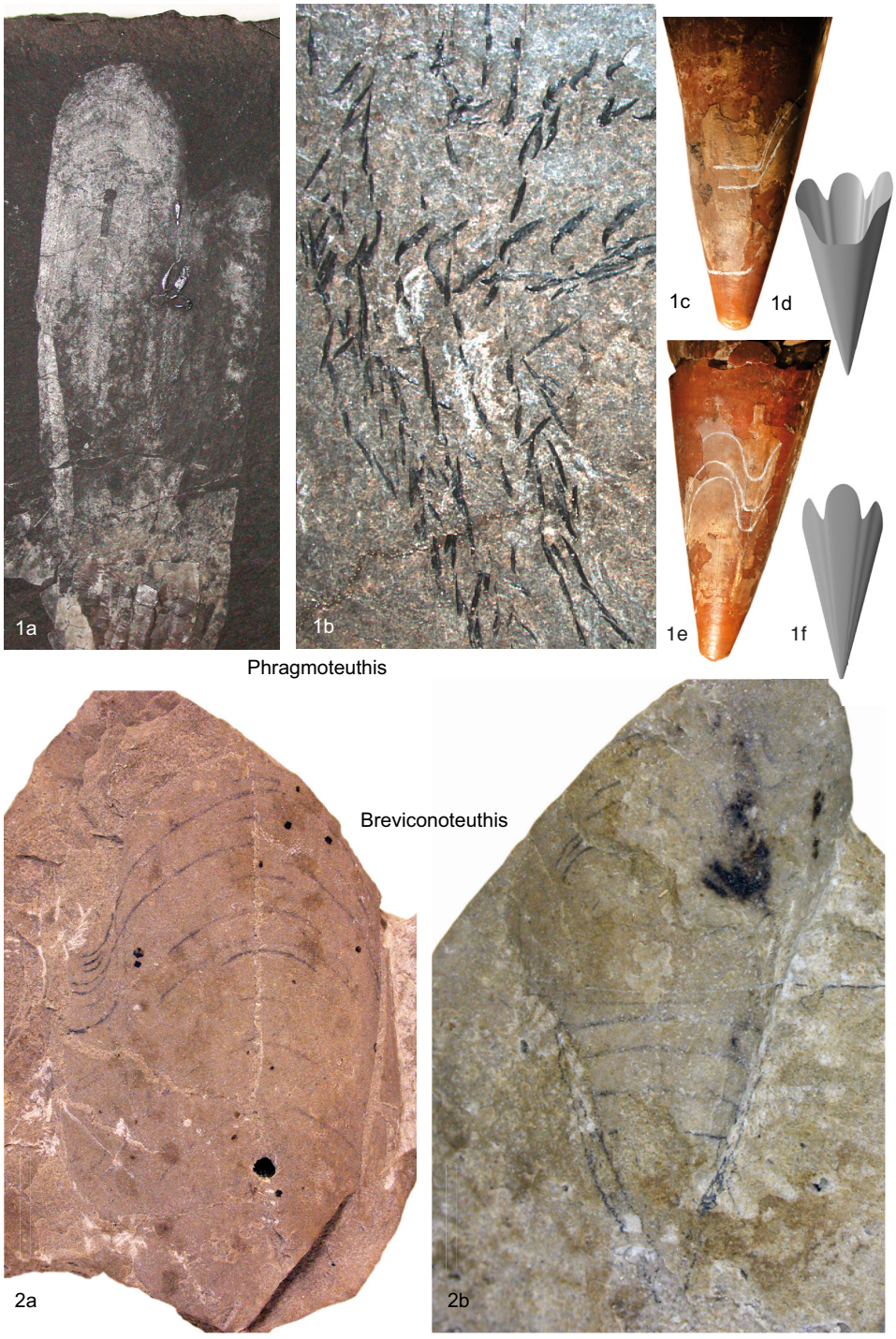

FIG. 2. Family Phragmoteuthidae (p. 3).

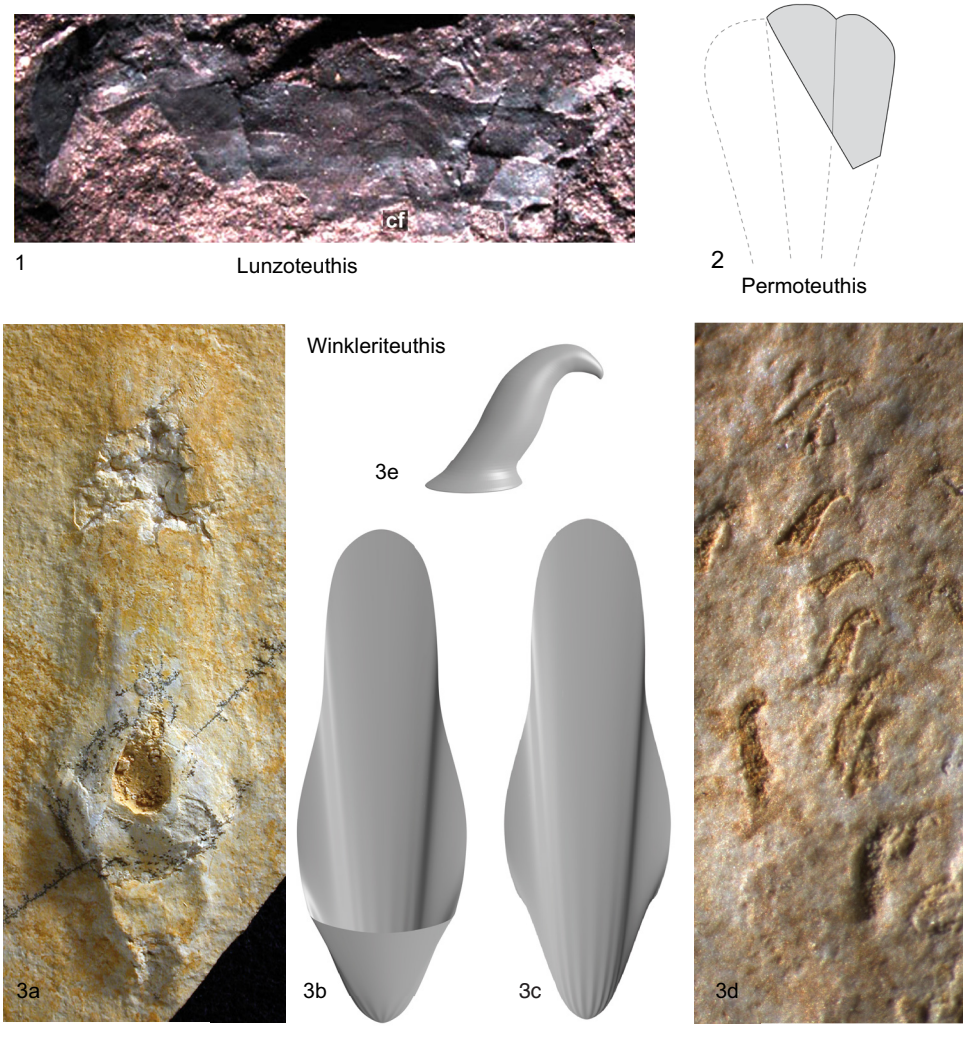

FIG. 3. Putative Phragmoteuthida (p. 3–5).

a–b, paratype, BSPG MC-22; *a,* entire specimen, ×1.2; *b,* close-up view of hooks, ×16 (Fuchs, Heyng, & Keupp, 2013, fig. 2); *c–d,* reconstruction of the shell, ventral (*c*) and dorsal (*d*) views (new); *e,* 3-D reconstruction of a hook (new).

Zugmontites REIS, 1907, p. 148 [**Z. mojsisovicsi* REIS, 1907, p. 148; SD BÜLOW-TRUMMER, 1920, p. 75]. Phragmocone very small to small, cyrtoconic, laterally compressed; apical angle about 38°; ratio of chamber length to diameter about 0.30; siphuncle marginal; prostracum unknown; rostrum unknown. *Middle Triassic (upper Anisian):* Austria.——FIG. 4*a–c. *Z. mojsisovicsi,* upper Anisian, Wettersteinkalk, Ehrwald, Austria, holotype, BSPG 1901 II 508; ventral (*a*), lateral (*b*), and dorsal (*c*) views, ×2 (new; photo by A. Nützel).

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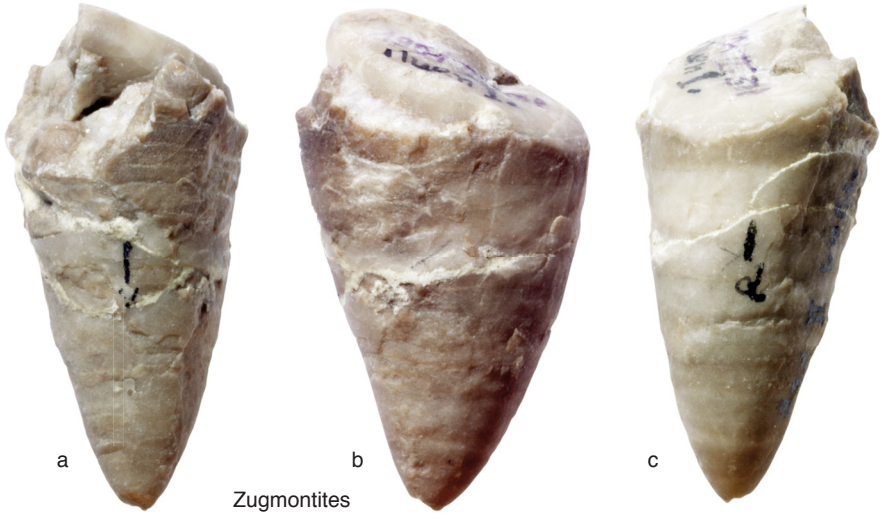

FIG. 4. Putative Phragmoteuthida (p. 5).

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