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ICHNOGENUS *PHOLEUS* FIEGE, 1944, REVISITED

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ABSTRACT—The ichnogenus *Pholeus* Fiege, 1944, is a common constituent of the Lower Muschelkalk (Middle Triassic) carbonates of the Germanic Basin, where it occurs in the upper part of shallowing upward cycles. It is restricted to a marly limestone lithofacies and is commonly associated with omission and erosion surfaces. The dwelling structures (domichnia) were created in a shallow-marine to lagoonal paleoenvironment in an intertidal to shallow subtidal setting. New material from Thuringia and Lower Saxony makes a re-evaluation of *Pholeus* possible and confirms the validity of this ichnogenus. Certain features, such as general form, wall, lining, and branching differentiate it from similar trace fossils. In addition to the already described *P. abomasoformis*, three new ichnospecies are named for distinctive forms: *P. bifurcatus*, *P. platiformis*, and *P. elongatus*. Based on geometry, size, and wall lining, the burrow producers were most probably decapod crustaceans. Many similarities to modern burrows of *Callianassa* sp., *Neocallichirus grandimina*, and *Nephrops norvegicus* suggest thalassinian shrimps and lobsters as likely tracemakers of *Pholeus* burrows. Compound burrow systems and retrusive burrow parts with spreiten-like structures are common and point to an upward shifting of the burrows related to certain sediment input in relation to tidal currents.

INTRODUCTION AND GEOLOGIC SETTING

The trace fossil *Pholeus* is a common constituent of the Lower Muschelkalk (Middle Triassic) carbonates of the Germanic Basin and has been reported from several regions (Reis, 1910, 1921; Rieth, 1932; Fiege, 1944; Kruck, 1974; Paul and Franke, 1977; Szulc, 1991; Dünkel and Vath, 1991; Knaust, 1998, in press). In contrast, only few reports exist from other geologic settings (Verma, 1970; Banerjee, 1982; Akpan and Nyong, 1987), and these need to be verified. Although *Pholeus* remains are poorly known, this trace fossil seems to be a sensitive paleoenvironmental indicator. Since its description by Fiege (1944), abundant and better-preserved material has been collected from several outcrops, allowing for a more detailed and emended description of the ichnogenus as well as for the erection of three new ichnospecies. Specific features such as retrusive burrow parts indicate a proximal-ward movement of the producer in relation to an unsteady rate of deposition.

The material described in this paper was collected in different outcrops of Thuringia and Lower Saxony, where the Lower Muschelkalk carbonates were deposited on carbonate platforms within a shallow epicontinental sea. In the study area, it reaches a thickness of about 100 m and consists mainly of marly limestone interbedded with bioclastic and intraclastic limestone beds (Fig. 1). In terms of sequence stratigraphy, the Lower Muschelkalk is part of a third-order sequence and comprises the transgressive and highstand systems tracts, separated from each other by the maximum flooding surface between the Terebratula Beds (Aigner and Bachmann, 1992). The lithological and ichnological data allow a further subdivision into small-scale shallowing- and deepening-upward cycles, in which the shallowest parts are characterized by the *Pholeus-Thalassinoides* ichnofabric (Knaust, 1998). The associated ichnofauna often contains *Rhizocorallium irregulare*. *Pholeus* occurs in marly limestone with a flasery and platy texture (Knaust, in press) and the associated lithofacies contains features such as algal lamination and desiccation cracks. The burrows are common below omission surfaces (firmgrounds) and erosion structures (e.g., gutter and pot casts, see Fiege, 1944, p. 403) at the base of limestone beds. No indications of mounds around the apertures have been seen in the outcrop; instead, wrinkle marks (''Runzelmarken'') occur at the top of some well-preserved apertures.

MATERIAL AND METHODS

More than 60 single and compound burrows as well as several fragments of burrows have been studied in about 20 Lower Muschelkalk outcrops of Thuringia and Lower Saxony. Weathered rock faces and glacially polished walls allow partial and complete excavation of the specimens. The individual burrows are exclusively preserved as exichnia casts or steinkerns of marly limestone and are often broken. In general, they can be easily collected segment by segment from the surrounding sediment and then reassembled, so that the whole morphology and branching becomes visible.

As shown below, the burrows have significant dimensions, and Fiege (1944) applied several measurements to characterize *Pholeus* (see Fig. 2). According to the material studied in this paper, the parameters c, d and f sensu Fiege (1944) are poorly defined for reasons of great variability, whereas the dimensions h and i seem to be more important (Fig. 2). In addition, the ratio between height and width of the horizontal part (e/g) is also used in statistic analysis (Fig. 3), provided that no notable deformation or compaction affected the burrow. Size data for measured burrows are given in Table 1, with each part of compound burrow systems listed separately. The type material is placed in the Geological Collection of the Institute of Geology and Paleontology at the University of Göttingen, Germany (Sample-Numbers IMGP Gö 1225-1 through IMGP Gö 1225-10).

SYSTEMATIC ICHNOLOGY

Ichnogenus Pholeus Fiege, 1944

Spongeliomorpha. Reis, 1910, p. 256–259, pl. 11, figs. 12, 14, 15, 18–20, 22 (in part); Reis, 1911, p. 12, fig. 1 (in part); Reis, 1921, p. 231–236, fig. 2.

Spongites-artige Fucoiden. Rieth, 1932, p. 27–29, figs. 25–27.

Pholeus abomasoformis Fiege, 1944, p. 401–416, fig. a (holotype).

Thalassinoides visurgiae Fiege, 1944, p. 416–421, fig. 4 (uncertain).

Pholeus abomasoformis Fiege. Häntzschel, 1962, p. W208, fig. 128,3; Häntzschel, 1965, p. 108; Häntzschel, 1975, p. W93, fig. 59,1; Knaust, 1998, p. 27, figs. 3b, 4e; Knaust et al., 1999, p. 232, fig. 6b.

Pholeus isp. Knaust et al., 1999, p. 233, fig. 7c.

Pholeus robustus Verma, 1970, p. 39, fig. 7 (non).

Pholeus abamasoformis Fiege. Kruck, 1974, p. 141–143, fig. 3–7, pl. 15, fig. 2.

Pholeus. Paul and Franke, 1977, p. 153, 162, 168, fig. 1 (not figured); Kamola, 1984, p. 532, figs. 9, 10 (non); Dünkel and Vath, 1991, p. 92, 93, 96, 99 (not figured); Szulc, 1991, p. 59, figs. 44, 58, 73 (not figured).

Pholeus Fiege. Banerjee, 1982, p. 96, figs. 5b, 6b (uncertain); Akpan and Nyong, 1987, p. 179, fig. 3 (uncertain).

Type species.—*Pholeus abomasoformis* (Fiege, 1944).

Emended diagnosis.—Single or complex U-formed, cylindrical

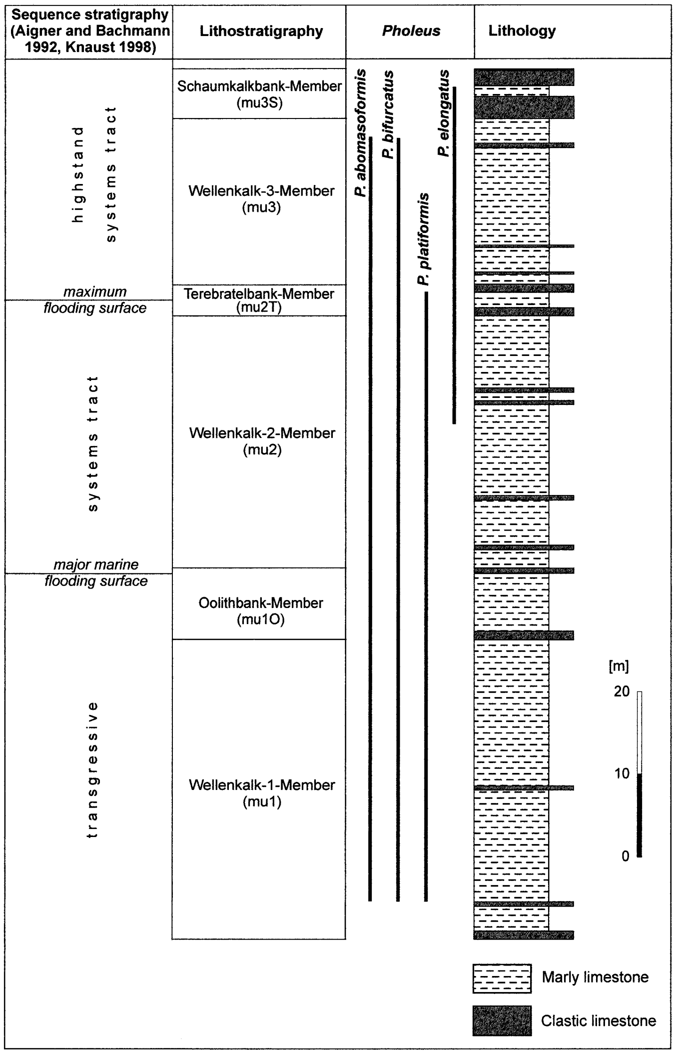


FIGURE *1*—Lithostratigraphic summary of the Lower Muschelkalk succession in the study area, showing distribution of the described *Pholeus* ichnospecies.

or elliptical, lined burrow system with a straight or curved longitudinal axis parallel to bedding, generally leading into an oblique burrow toward the surface; opposite end closed and rounded, with a smaller, rising vertical to subvertical shaft.

Discussion.—An extension of the ichnogenus *Pholeus* is made mainly on the basis of general form and branching, which are considered major criteria in classifying modern thalassinidean burrows produced by several crustacean species (Dworschak and Ott, 1993). In addition to *P. abomasoformis*, the present material from the Muschelkalk allows classification of *Pholeus* into several ichnospecies (Fig. 4). Apart from *P. robustus* Verma (1970), no other ichnospecies of *Pholeus* has been described hitherto. Because *P. robustus* lacks features such as an oblique burrow and a smaller vertical one, it should be excluded from the ichnogenus *Pholeus*. *Pholeus* described by Kamola (1984) as a W-shaped burrow with additional upward branching arms, but without the smaller vertical shaft and no apparent lining, must be also assigned to another ichnotaxon. Other forms described by Banerjee (1982) and Akpan and Nyong (1987) are mainly horizontal burrows and may herein be assigned to *Pholeus* with some reservation.

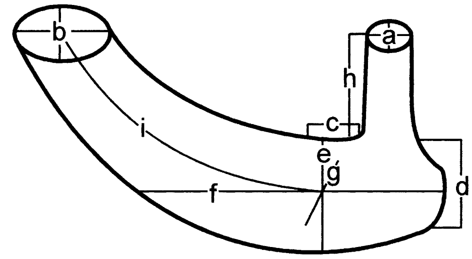


FIGURE *2*—Burrow measurement parameters of *Pholeus* used in the present study (after Fiege, 1944). a = diameter at the end of the vertical/subvertical shaft, b = diameter at the end of the oblique burrow, c = distance between vertical/subvertical shaft and oblique burrow, d = height of the closed end just below the vertical/subvertical shaft, e = height of the horizontal part, f = length of the horizontal part, g = width of the horizontal part, h = height of the vertical/subvertical shaft, i = total length of the entire horizontal and oblique burrow.

Ichnospecies PHOLEUS ABOMASOFORMIS (Fiege, 1944)
Figure 5.1–5.2

Spongeliomorpha. REIS, 1910, p. 256–259, pl. 11, figs. 18–20 (in part).
Pholeus abomasoformis FIEGE, 1944, p. 401–416, fig. a (holotype).
Pholeus abomasoformis FIEGE. HÄNTZSCHEL, 1962, p. W208, fig. 128,3; HÄNTZSCHEL, 1965, p. 108; HÄNTZSCHEL, 1975, p. W93, fig. 59,1; KNAUST, 1998, p. 27, figs. 3b, 4e (in part); KNAUST et al., 1999, p. 232, fig. 6b.
Pholeus robustus VERMA, 1970, p. 39, fig. 7 (non).
Pholeus abamasoformis Fiege. KRUCK, 1974, p. 141–143, figs. 3–7, pl. 15, fig. 2.
Pholeus, PAUL AND FRANKE, 1977, p. 153, 162, 168, fig. 1 (not figured, uncertain); DÜNKEL AND VATH, 1991, p. 92, 93, 96, 99 (not figured, uncertain); SZULC, 1991, p. 59, figs. 44, 58, 73 (not figured, uncertain).
Pholeus Fiege. BANERJEE, 1982, p. 96, figs. 5b, 6b (uncertain); AKPAN AND NYONG, 1987, p. 179, fig. 3 (uncertain).

Emended diagnosis.—U-formed, unbranched burrow with a vertically extended elliptical horizontal part, an oblique cylindrical part, and a smaller cylindrical shaft vertical or subvertical in cross-section.

Description.—The thicker main part of the U-shaped casts of *Pholeus abomasoformis* bends off to the sediment surface at a more or less shallow (oblique) to steep (subvertical) angle. It is oval in cross section with an e/g ratio of 1.0–1.9 (mean: 1.2). The

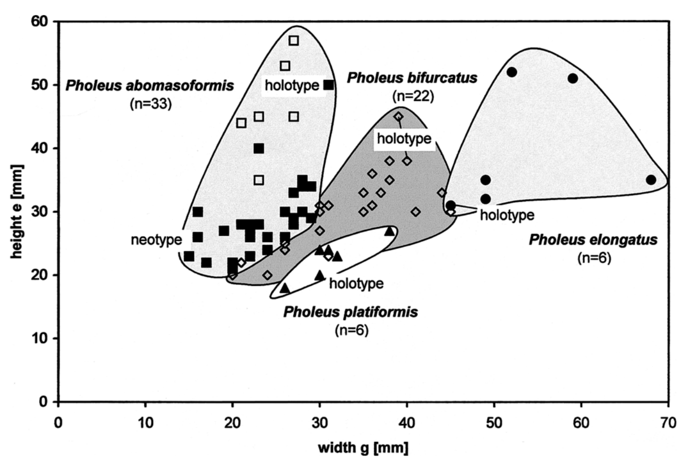


FIGURE *3*—Scatter diagram showing the height/width (e/g) ratio of the main burrow part in all described *Pholeus* ichnospecies (open squares in the *P. abomasoformis* area are related to burrows with retrusive spreiten structures).

TABLE *1*—Size data for the measured burrows. Measurements *a* through *i* refer to Fig. 4 (c = compacted, spr = spreiten).

Type number	Specimen number	Member	a	b	c	d	e	f	g	h	i	e/g	Ichnospecies
	Specimen 1 after Fiege (1944)		22 × 19	31 × 27	72	42	50	129	31	—	—	1,6	*P. abomasoformis*
	Specimen 2 after Fiege (1944)		20 × 20	? × ?	>40	38	42	>98	38	—	—	1,1	
	Specimen 3 after Fiege (1944)		25 × 28	28 × 30	45	42	42	98	30	—	—	1,4	
	Specimen 4 after Fiege (1944)		17 × 19	28 × 30	80	(c) 25	(c) 25	125	36	—	—	(c) 0,7	
	BB-1	mu3S	—	—	—	—	(c) 49	—	43	—	—	(c) 1,1	
	BB-2	mu3S	—	—	—	—	52	—	52	—	—	1,0	*P. elongatus*
	ELL-1	mu1	23 × 27	27 × 27	~35	—	—		33	(c) >85	(c) >156	—	*P. abomasoformis*
	ELV-1	mu2T	15 × 17	27 × 29	~58	10	24		26	—	>132	0,9	*P. bifurcatus*
	ELV-2 (part one)	mu3	19 × 21	29 × 35	56	2	36		36	—	>111	1,0	*P. bifurcatus*
	ELV-2 (part two)	mu3	—	—	—	—	33		37	—	>93	0,9	*P. bifurcatus*
	ELV-3	mu2T	14 × 19	27 × 31	~36	0	(spr) 57		27	>35	>113	(spr) 2,1	*P. abomasoformis*
	ELV-4	mu2T	11 × 12	23 × 22	~21	0	(spr) 44		21	>34	>75	(spr) 2,1	*P. abomasoformis*
	ELV-5	mu2T	18 × 5	30 × 29	~12	0	(spr) 35		23	>26	>67	(spr) 1,5	*P. abomasoformis*
	ELV-6 (lower part)	mu2	26 × 21	27 × 29	24	12	35		28	—	>99	1,3	*P. abomasoformis*
	ELV-6 (upper part)	mu2	18 × 18	29 × 28	~7	8	26		22	—	>81	1,2	*P. abomasoformis*
	ELV-7	mu3	19 × 16	30 × 28	~16	7	28		27	—	>104	1,0	*P. abomasoformis*
	ELV-8	mu3	9 × 9	18 × 20	~10	7	22		20	—	>67	1,1	*P. abomasoformis*
	ELV-9	mu2	15 × 16	25 × 22	~22	<8	28		27	—	>81	1,0	*P. abomasoformis*
	ELV-10	mu3	16 × 13	30 × 26	29	7	30		26	—	>109	1,1	*P. abomasoformis*
	ELV-11	mu2	—	39 × 35	~40	—	29		29	—	>101	1,0	*P. abomasoformis*
	ELV-12	mu2T	30 × 28	—	—	—	—		—	—	—	—	
	ELV-13	mu3	—	—	—	—	>22		25	—	>75	>0,9	*P. abomasoformis*
IMGP Gö 1225-5	GSD-1	mu1	(c) 16 × 19	—	—	—	20	—	30	(c) >51	>160	0,7	*P. platiformis*
	GSD-2	mu1	24 × 21	(c) 37 × 33	?40	19	30	90	35	—	>146	0,9	*P. bifurcatus*
IMGP Gö 1225-4	GSD-3 (lower part)	mu1	23 × 22	38 × 40	59	21	30	140	41	>49	220	0,7	*P. bifurcatus*
IMGP Gö 1225-4	GSD-3 (middle part)	mu1	22 × 23	22 × 22	?22	—	20	70	24	>58	140	0,8	*P. bifurcatus*
IMGP Gö 1225-4	GSD-3 (upper part)	mu1	18 × 21	36 × 32	54	22	33	90	35	40	175	0,9	*P. bifurcatus*
	GSD-4 (lower part)	mu1	24 × 22	26 × 26	?60	13	23	95	31	—	161	0,7	*P. bifurcatus*
	GSD-4 (middle part)	mu1	19 × 20	35 × 36	?25	15	31	75	31	43	126	1,0	*P. bifurcatus*
	GSD-4 (upper part)	mu1	—	30 × 33	—	—	20	—	20	—	>101	1,0	*P. bifurcatus*
	GSD-5	mu1	14 × 20	20 × 23	20	12	21	60	20	—	97	1,0	*P. abomasoformis*
	GSD-6	mu1	—	—	—	—	—	—	—	(c) >185	—	—	
	GSD-7	mu1	—	—	—	—	—	—	—	(c) >145	—	—	
IMGP Gö 1225-7	GSD-8	mu1	—	—	—	—	27	—	38	—	>284	0,7	*P. platiformis*
	GSD-9 (lower part)	mu1	—	—	—	—	30	—	45	—	140	0,7	*P. bifurcatus*
	GSD-9 (upper part)	mu1	21 × 20	—	28	(c) 13	31	—	36	—	118	0,9	*P. bifurcatus*
	GSD-10	mu1	19 × 20	—	38	16	>25	100	35	50	>121	>0,7	
	GSD-11	mu1	22 × 20	28 × 32	20	17	31	77	30	(c) >84	>182	1,0	*P. bifurcatus*
	GSD-12	mu2	—	—	—	—	24	—	30	—	>232	0,8	*P. platiformis*
	GD-1	mu2	50 × 38	—	?70	—	27	110	30	—	>255	0,9	*P. bifurcatus*
IMGP Gö 1225-8	GD-2	mu3	?32 × 20	51 × 28	—	22	31	—	45	—	>700	0,7	*P. elongatus*
	GD-3	mu2	—	—	—	—	28	—	23	—	—	1,2	*P. abomasoformis*
	HHN-1 (part one)	mu3	—	24 × 22	69	2	(spr) 45		27	—	>142	(spr) 1,7	*P. abomasoformis*
	HHN-1 (part two)	mu3	—	28 × 21	—	—	—		—	—	—	—	*P. abomasoformis*
	HHN-2	mu3	12 × 12	—	~23	3	(c) 17		20	—	>56	(c) 0,9	*P. abomasoformis*
	HHN-3 (lower part)	mu3	15 × 16	30 × 29	25	—	26		26	—	95	1,0	*P. abomasoformis*
	HHN-3 (upper part)	mu3	11 × 10	19 × 17	18	6	27		19	—	70	1,4	*P. abomasoformis*
	HHN-4	mu3	12 × 12	20 × 19	26	1	27		22	(c) >52	>115	1,2	*P. abomasoformis*
	HHN-5	mu3	13 × 12	28 × 31	13	10	30		28	>56 (c)	>115	1,1	*P. abomasoformis*
	HHN-6 (part one)	mu3	21 × 22	—	—	—	25		26	>35	—	1,0	*P. bifurcatus*
	HHN-6 (part two)	mu3	—	—	—	—	22		21	—	—	1,0	*P. bifurcatus*
	HF-1	mu2	—	—	—	—	35	—	49	—	>425	0,7	*P. elongatus*
IMGP Gö 1225-6	JZ-1	mu1	—	29 × 19	?25	18	18	100	26	—	115	0,7	*P. platiformis*
	LGF-1	mu3	30 × 27	—	—	—	34	>101	28	—	>121	1,2	*P. abomasoformis*
	OSS-1	mu3	13 × 12	38 × 41	~48	1	(c) 27		32	33	142	(c) 0,8	*P. abomasoformis*
	OSS-2	mu3	14 × 11	19 × 17	~13	5	22		17	—	>65	1,3	*P. abomasoformis*
	OSS-3	mu3	9 × 8	12 × 12	22	10	23		15	>23	>91	1,5	*P. abomasoformis*
	RD-1	mu3	—	—	—	—	>27	—	50	—	>435	>0,5	
	RD-2	mu3	11 × 12	22 × 22	104	—	(c) 21	147	20	36	(c) >160	(c) 1,0	
	RD-3	mu3	(c) 14 × 15	(c) 20 × 21	36	9	28	84	22	(c) 38	(c) 114	1,3	*P. abomasoformis*

TABLE *1*—Continued.

Type number	Specimen number	Member	a	b	c	d	e	f	g	h	i	e/g	Ichnospecies
IMGP Gö 1225-9	RD-4	mu3	—	—	—	—	51	—	59	—	>245	0,9	*P. elongatus*
IMGP Gö 1225-10	RD-5 (main part)	mu3	(c) 10 × 12	—	—	—	>50	—	63	(c) 58	>310	>0,8	
IMGP Gö 1225-10	RD-5 (sec. burr.)	mu3	10 × 10	—	?43	—	—	—	33	(c) 50	>85	—	
	RD-6	mu3	(c) 17 × 18	—	—	—	—	—	—	(c) >247	—	—	
IMGP Gö 1225-3	SB-1 (part one)	mu1O	18 × 18	26 × 25	75	25	38	95	38	(c) 149	245	1,0	*P. bifurcatus*
IMGP Gö 1225-3	SB-1 (part two)	mu1O	26 × 24	30 × 25	?55	—	33	85	44	—	240	0,7	*P. bifurcatus*
IMGP Gö 1225-3	SB-1 (part three)	mu1O	—	34 × 25	90	?13	35	79	38	—	170	0,9	*P. bifurcatus*
IMGP Gö 1225-2	SB-2 (part one)	mu1O	26 × 21	30 × 29	?53	?14	38	90	40	—	>170	0,9	*P. bifurcatus*
IMGP Gö 1225-2	SB-2 (part two)	mu1O	(c) 30 × 29	35 × 34	?60	—	45	130	39	(c) 52	(c) 210	1,1	*P. bifurcatus*
	SB-3	mu1O	?18 × ?21	29 × 21	74	8	30	77	30	—	197	1,0	*P. bifurcatus*
	SDH-1	mu3?	13 × 13	23 × 17	42	4	23		22	—	109	1,0	*P. abomasoformis*
	SDH-2	mu3?	17 × 14	19 × 24	15	>8	33		27	—	>80	1,2	*P. abomasoformis*
	TC-1	mu2T	?14 × ?14	—	—	?22	24	—	31	—	>157	0,8	*P. platiformis*
IMGP Gö 1225-1	VB-1	mu2	9 × 9	20 × 28	?12	?14	26	48	16	(c) >30	76	1,6	*P. abomasoformis*
	VB-2	mu2	—	(c) 21 × 18	?26	?10	30	50	16	—	(c) 82	1,9	*P. abomasoformis*
	VB-3 (lower part)	mu1	(c) 12 × 11	(c) 26 × 30	31	20	40	72	23	(c) >73	119	1,7	*P. abomasoformis*
	VB-3 (upper part)	mu1	(c) 12 × 13	(c) 23 × 23	27	—	27	63	22	(c) 41	(c) >83	1,2	*P. abomasoformis*
	VB-4 (lower part)	mu2	(c) 14 × 13	28 × 25	61	7	(c?) 19	103	29	—	170	(c?) 0,7	
	VB-4 (upper part)	mu2	(c) 17 × 17	31 × 30	43	—	29	86	27	(c) 63	145	1,1	*P. abomasoformis*
	VB-5	mu1	—	—	26	0	24	70	24	—	> 86	1,0	*P. abomasoformis*
	VB-6	mu1	—	17 × 18	—	—	(spr) ~53	~90	26	34	>119	(spr) 2,0	*P. abomasoformis*
	05/01/24/01		—	—	—	—	35		68	—	>245	0,5	*P. elongatus*
	05/01/12/03		19 × 11	—	—	—	23		32	~69	>147	0,7	*P. platiformis*
	05/01/16/01		—	—	—	—	32		49	—	>500	0,6	*P. elongatus*
	05/01/16/02	mu1O	—	—	—	~10	(spr) ~45		23	~17	100	(spr) 2,0	*P. abomasoformis*
	05/01/10/01	mu3	23 × 16	29 × 27	~30	—	34		29	26	116	1,2	*P. abomasoformis*
	05/01/12/01		13 × 13	27 × 23	~23	>8	26		24	>23	113	1,1	*P. abomasoformis*
	05/01/12/02		17 × 13	16 × 16	~30	0	28		21	>19	>164	1,3	*P. abomasoformis*

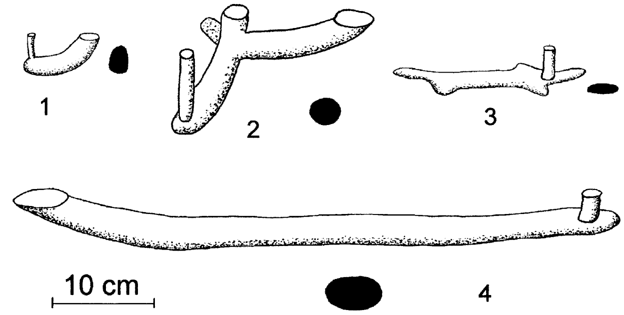


FIGURE *4*—Sketch with a summary of the described *Pholeus* ichnospecies and their corresponding cross sections. *1*, *P. abomasoformis*. *2*, *P. bifurcatus*. *3*, *P. platiformis*. *4*, *P. elongatus*.

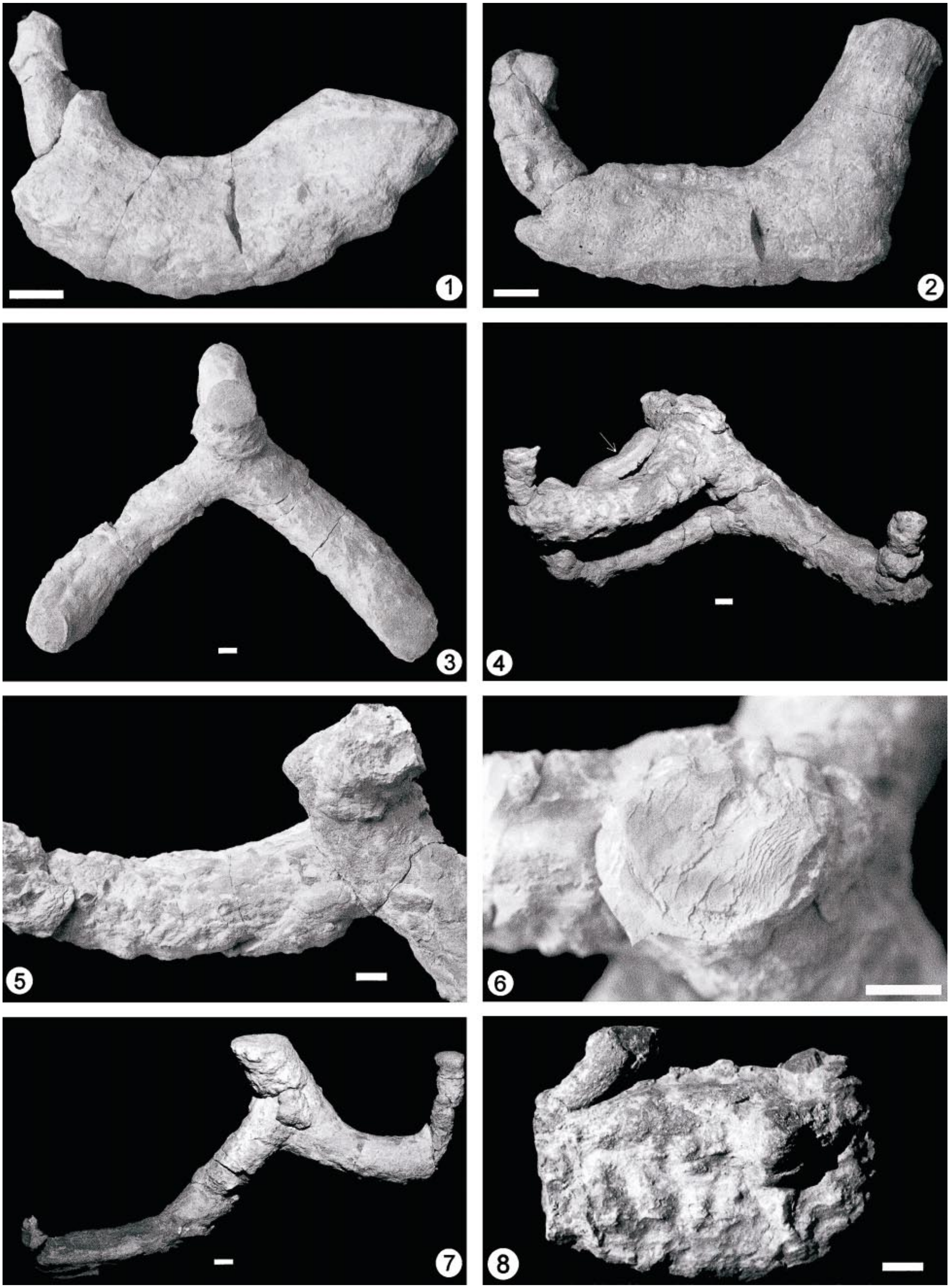
total length of the entire horizontal and oblique burrow (i) is between 70 and 170 mm. On the bedding surface, there are generally two openings visible: a bigger oval one and a smaller circular one. In plan view, several specimens show minor changes in the generally linear orientation with either a sinistral or a dextral turn. In rare cases, vague ornaments of shallow grooves and ridges are oriented perpendicular to the burrow axis. The wall is irregularly lined with several mud pellets (rounded to knobby flakes), commonly between 4–8 mm wide and 1–3 mm high. Typically different burrows are connected in compound burrows. This connection appears in various ways but is always in different vertical levels owing to shifting of the burrow. In this case, swellings occur or mudflakes are plastered at the junction points. Occasionally, elongated and slightly curved secondary burrows and trails of *Archaeonassa fossulata* (about 1 mm wide) occur. Owing to compactional processes, the more vertical burrow parts may be stacked into each other and commonly are affected by stylolites. Pseudomorphs of small celestine crystals (0.5–1 mm wide and up to more than 10 mm long) are scattered within the muddy limestone matrix.

Material examined.—In addition to several more or less complete single specimens a few compound two-burrow systems also have been found. The holotype described by Fiege (1944) was not to be found either in the Geological Collection of the Institute of Geology and Paleontology at the University of Göttingen or in the Geological and Paleontological Institute at the University of Kiel. However, specimen IMPG Gö 1225-1 is designated to be the neotype of *Pholeus abomasoformis*. The neotype specimen was found in the limestone quarry Vogelbeck (Oppermann Company), Lower Saxony, which is situated about 20 km north of the locality Nörten where Fiege collected his holotype. Type horizon is Wellenkalk-2-Member, about 0.5 m above the Upper Oolith-Bed.

Discussion.—*Pholeus abomasoformis* differs from *P. bifurcatus* by being a more simple, unbranched burrow with a high-oval cross-section (e/g ratio more than 1). *Pholeus platiformis* is characterized by blind-ending side branches and a flat cross-section (e/g ratio less than 0.8). *Pholeus elongatus* has a flat-oval cross-section (e/g ratio less than 1) and contrasts to *P. abomasoformis* by its much larger size.

Ichnospecies PHOLEUS BIFURCATUS new ichnospecies
Figure 5.3–5.6

Spongeliomorpha. REIS, 1910, p. 256–259, pl. 11, fig. 14 (in part); REIS, 1911(?), p. 12, fig. 1 (in part); REIS, 1921, p. 231–236, fig. 2 (in part).
Spongites-artige Fucoiden. RIETH, 1932, p. 27–29, figs. 25–27 (in part).
Thalassinoides visurgiae FIEGE, 1944, p. 416–421, fig. 4 (uncertain).
Pholeus isp. KNAUST et al., 1999, p. 233, fig. 7c.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Diagnosis.—Complex *Pholeus*, essentially cylindrical, comprising a branched burrow with dichotomous or Y-shaped bifurcations parallel to bedding, and consisting of two or more oblique and slightly curved arms which join together in a relatively short central shaft having approximately the same diameter, as well as a narrower and longer vertical shaft at the distal end.

Description.—From a central position, the main shaft, having a diameter of about 20–30 mm, descends vertically into the sediment, where two or three tunnels branch off in star-like fashion at a horizontal angle of about 120 degrees. One of these shallow U-like tunnels may end distally in an opening to the sediment surface, whereas another one bears the *Pholeus*-typical vertical shaft which is smaller in diameter. The third tunnel, which is developed at the opposite side (Fig. 5.4), may be missing or became stunted (Fig. 5.3). The variability of this ichnospecies also includes another tunnel starting from the distal end of a common tunnel, or tunnels that are arranged in different tiers. Horizontal bending of the tunnels is common. The cross-section of the tunnels is more or less circular with an e/g ratio between 0.7 and 1.1 (mean: 1.1) and the total length of the several burrow parts reaches up to more than 255 mm. Wrinkle marks are preserved in some of the openings at the bedding surface (Fig. 5.6). Irregular mud pellets commonly occur at the burrow wall and are up to 12 mm wide and 4 mm high (Fig. 5.5). In one instance (Fig. 5.4), a fourth and much smaller tunnel appears as the deepest tier owing to branching off from a main tunnel. Because its vertical shaft runs through a shallower tunnel to the surface, it may be interpreted as a secondary colonization of *Pholeus*. A horizontal spreiten burrow of *Rhizocorallium irregulare* with well-developed scratch ornament at the wall also affects the same shallow tunnel. Curved to contorted burrows of *Planolites montanus* are more common secondary trace fossils, 1–4 mm wide and several cm long, and visible at the tunnel wall (Fig. 5.5). Elongated groove-like trace fossils that belong to *Archaeonassa fossulata*, up to several cm long and 2–5 mm wide, also occur. Owing to diagenetic effects, the vertical burrow parts commonly are compacted and may bear stylolites, whereas the inner parts of the tunnels especially are affected by sponge-like growth of celestine crystals.

Etymology.—Species name *bifurcatus* reflects the bifurcations of the burrow system.

Types.—Holotype, IMPG Gö 1225-2, Wellenkalk-2-Member, Oolith-Beds, abandoned quarry north of the village Saalborn near Bad Berka, Thuringia. Paratypes, IMPG Gö 1225-3 and -4.

Discussion.—*Pholeus bifurcatus* can be differentiated from the smaller ichnospecies *P. abomasoformis* and from the larger ichnospecies *P. elongatus* by its dichotomous or Y-shaped bifurcations and an approximately circular cross-section (e/g ratio about or less than 1). The side branches of the flat ichnospecies *P. platiformis* are short and end blindly.

Ichnospecies PHOLEUS PLATIFORMIS new ichnospecies
Figure 6.1–6.4

Spongeliomorpha. REIS, 1910, p. 256–259, pl. 11, fig. 15 (in part).

Diagnosis.—Simple, predominantly horizontal, essentially flat and shallow U-formed burrow with blindly-ending side branches as well as one (or more?) smaller vertical shaft(s).

Description.—Just five specimens of *Pholeus platiformis* have been found, all of them are flat in cross-section and show a relatively narrow main burrow with short irregular junctions in plan view. Total burrow length varies between 115 and more than 284 mm with an e/g ratio of 0.7–0.8 (mean: 0.7). Because of the small number of specimens and preservation problems it is not yet clear if the main tunnel of *P. platiformis* runs to the surface or ends blindly. However, up to four short burrows branch off from the straight or slightly curved main part and end blindly after a few cm. The average angle between main burrow and off-branch is commonly around 120 degrees, but other angles also occur. Occasionally, off-branches show swellings at branching points and may be bent upward. Flaky pellets are arranged sporadically and are 2–8 mm wide and 1–2 mm high. The vertical shaft is smaller in diameter than the gallery and bears few pellets. Apart from a poorly preserved, dense community of ?*Planolites montanus* and *Chondrites* isp., other secondary burrows include freely winding forms of *Archaeonassa fossulata*, preserved as a trail either on the floor or even as a burrow within the filling of *Pholeus*. Although vertical shafts are deformed by compaction processes, the actual cross-section of the main burrow is not significantly affected from this.

Etymology.—Species name *platiformis* reflects the essentially flat appearance of the burrow.

Types.—Holotype, IMPG Gö 1225-5 from limestone quarry east of Geilsdorf near Stadtilm, Thuringia, Wellenkalk-1-Member. Paratypes, IMPG Gö 1225-6 and-7.

Discussion.—*Pholeus platiformis* is characterized by its flat cross-section, which differentiates from *P. abomasoformis*. In contrast to *P. platiformis* with blind-ending off-branches, *P. bifurcatus* has an approximately circular cross-section and long branches. *Pholeus elongatus* has a similar cross-section as *P. platiformis* but is generally unbranched and much longer.

Ichnospecies PHOLEUS ELONGATUS new ichnospecies
Figure 6.5–6.11

Spongeliomorpha. REIS, 1910, p. 256–259, pl. 11, figs. 12, 22 (in part).
Spongites-artige Fucoiden. RIETH, 1932, p. 27–29, figs. 25, 27 (in part).

Diagnosis.—Curved, predominantly horizontal, essentially flat or cylindrical, extended unbranched or branched *Pholeus* with an oblique end toward the surface and a smaller cylindrical vertical or subvertical shaft at the opposite end.

Description.—The collected material includes several incomplete burrows as well as some smaller fragments. Their length varies from 245 to 700 mm, but complete burrows may reach a total length of more than 1 m (up to 1.6 m according to observations in Poland made by Joachim Szulc, personal commun., 1999). All burrows are slightly curved and show a circular or flat-oval cross-section, which is commonly incompletely filled with sediment, affected by secondary burrows, or even compacted. However, the measured and calculated e/g ratio is approximately 0.5–1.0 (mean: 0.7). The opening of the oblique main burrow to

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FIGURE 5— *1*, *Pholeus abomasoformis*, neotype, IMPG Gö 1225-1, Wellenkalk-2-Member (about 0.5 m above the Upper Oolith-Bed) of quarry Vogelbeck, Lower Saxony. *2*, *P. abomasoformis*, RD-3, Wellenkalk-3-Member (about 5–6 m below the Lower Schaumkalk-Bed) of quarry Rittersdorf, Thuringia. *3*, *Pholeus bifurcatus* n. isp., holotype, IMPG Gö 1225-2, Oolithbank-Member of Saalborn, Thuringia. *4–6*, *P. bifurcatus*, paratype, IMPG Gö 1225-4, Wellenkalk-1-Member of quarry Geilsdorf, Thuringia. *4*, Complex branched burrow system with a smaller tunnel in the deeper tier (secondary colonization), as well as a secondary spreiten burrow of *Rhizocorallium irregulare* (arrow); *5*, burrow wall with irregular mud pellets and secondary burrows of *Planolites montanus*; *6*, central main opening with wrinkle marks. *7*, *P. abomasoformis*, VB-4, compound burrow due to growth or escaping of the producer, Wellenkalk-1-Member and Wellenkalk-2-Member of quarry Vogelbeck, Lower Saxony. *8*, *P. abomasoformis*, VB-6, equilibrium trace resulting in spreiten-like structures, Wellenkalk-1-Member of quarry Vogelbeck, Lower Saxony. Scale bar = 1 cm.

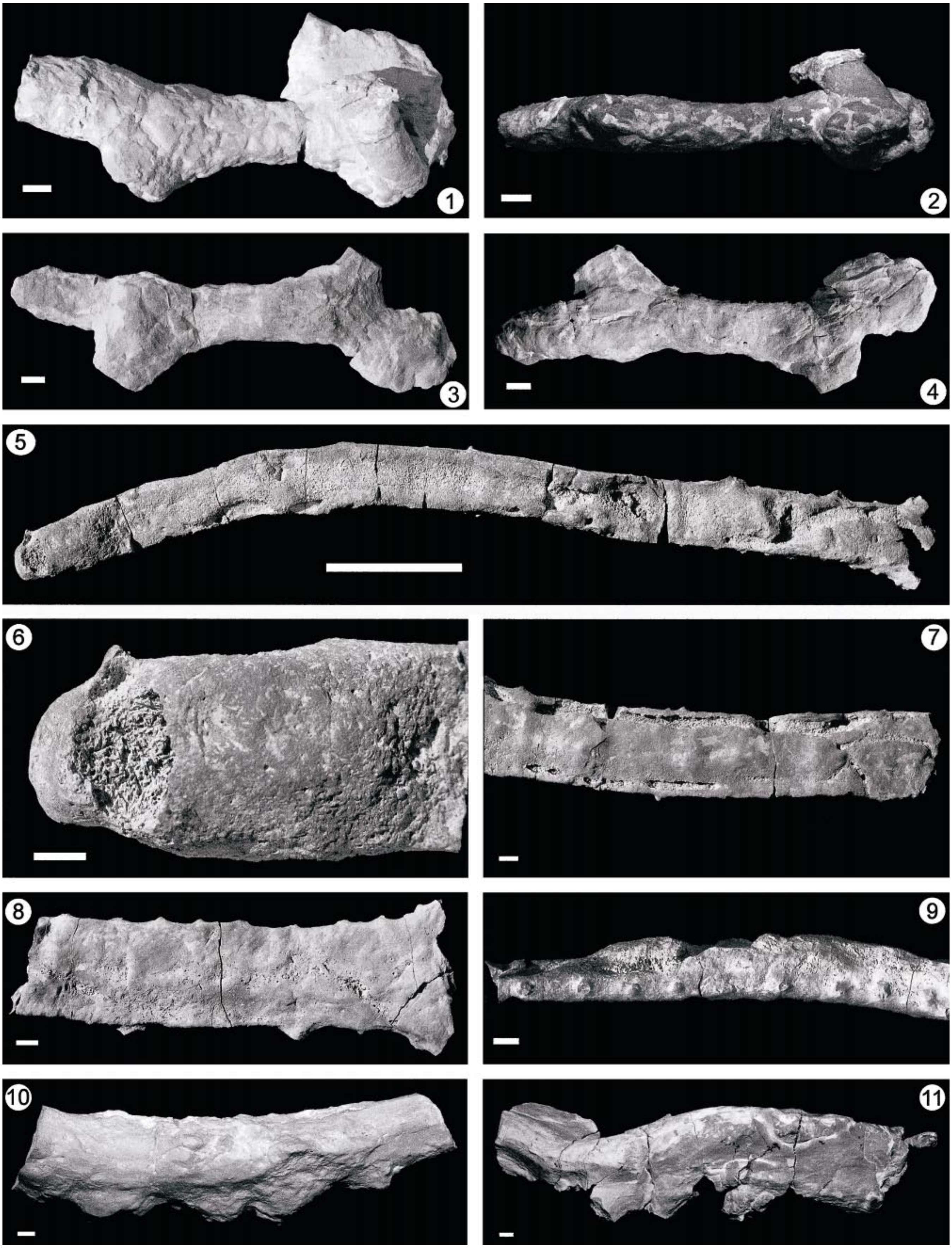
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TABLE *2*—Differentiation between *Pholeus* and similar ichnogenera.

	General form			Wall and lining		Branching	Fill	
	Simple burrow	Maze	Boxwork	Lining	Bioglyphs		Passive	Active
Pholeus	×	—	×	×	—	—/×	×	—
Spongeliomorpha	—	×	×	—	×	×	×	—
Ophiomorpha	—	×	×	×	—	×	×	—
Thalassinoides	—	×	×	—	—	×	×	—
Glyphichnus	×	—	—	—	×	—	×	—
Psilonichnus	×	—	×	—	—	×	×	—
Balanoglossites	×	×	—	—	×	—/×	×	—
Ctenopholeus	×	—	—	?	—	—/×	×	—
Cylindrichnus	×	—	—	×	—	—	?	?

the bedding surface is hardly visible but can be deduced from the outcrop situation. The smaller vertical shaft on the opposite end is rarely preserved, but its base is well marked by a hole in the specimen of the holotype. The reason for its absence is the spongy and porous appearance of the burrow due to the intense interior emplacement of celestine crystals. In addition to true branching, which was observed in one specimen, some fragments show bulbous extensions on the lateral margin reaching up to 100 mm length and 30 mm width. Apart from other pellets that sparsely line the wall, a patchy and regular pellet system accompanied both wall sides in some instances. Each mud pellet is between 4 and 20 mm wide and 2–10 mm high, and spaced at more or less regular distances of 15–30 mm. Secondary trails and burrows transect large portions of the *P. elongatus* burrow and rework its filling. They are traceable over more than 45 cm length and reach the considerable width of about 5–12 mm and belong to *Archaeonassa fossulata*. *Planolites montanus* also occurs as a secondary burrow and in one instance, *Pholeus elongatus* is reworked by *P. abomasoformis* (IMPG Gö 1225-10).

Etymology.—Species name *elongatus* reflects the elongated form of the trace fossil.

Types.—Holotype, IMPG Gö 1225-8 from limestone quarry Gutendorf near Bad Berka, Thuringia, Wellenkalk-3-Member, a few metres below the Schaumkalk-Member. Paratypes, IMPG Gö 1225-9 and-10.

Discussion.—*Pholeus elongatus* is by far the largest ichnospecies of *Pholeus* and differs from *P. abomasoformis* in having a flat-oval to circular cross-section (e/g ratio $\leq$1). In contrast to *P. elongatus*, the smaller forms *P. bifurcatus* and *P. platiformis* are always branched.

COMPARISON OF PHOLEUS WITH SIMILAR ICHNOGENERA

In a superficial way, *Pholeus* seems to be very similar to other well-known trace fossils that are most probably produced by crustaceans. However, some typical features such as the general burrow shape and lining differentiate *Pholeus* from other trace fossils (Table 2). *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides* commonly appear as complex boxworks and mazes (Bromley, 1996) and these dichotomously and T-branched burrows are comparable to *Pholeus bifurcatus*. They usually lack the U-formed burrow shape, which is developed in *Pholeus*, and also lack the typical smaller vertical shaft. In addition, *Ophiomorpha* is characterized by a lining showing distinct pellets externally (Frey et al., 1978; Ekdale, 1992) whereas *Spongeliomorpha* is unlined and bears a strong bioglyph of ridges. *Glyphichnus* differs from *Pholeus* by its deeply incised bioglyphs and regular U-shape (Bromley and Goldring, 1992). As mentioned by Frey et al. (1984, p. 344), most similarities exist between *Thalassinoides* and *Pholeus*, but in addition to the morphological difference mentioned above, *Thalassinoides* is unlined, whereas *Pholeus* has a distinct external lining of flakes. The ichnogenus *Psilonichnus* consists of predominantly vertical, unlined burrows ranging from irregular shafts to crudely J-, Y-, or U-shaped structures (Frey et al., 1984), and the much smaller *Balanoglossites* of the Muschelkalk is characterized by an irregular-shaped burrow system with occasional scratch marks and diagenetical haloes around the burrows. Following *Pholeus*, Seilacher and Hemleben (1966) describe *Ctenopholeus*, which is somewhat morphologically similar to *Pholeus*, but consists of a long horizontal tunnel-like burrow with rare horizontal branches and vertical shafts rising at equal intervals (Häntzschel, 1975). Kennedy (1967) gave a similar description in his burrow type A and compared it with *P. abomasoformis*. Simple U-shaped and concentrically-laminated burrows are generally referred to *Cylindrichnus concentricus*, but differ from *Pholeus* by the absence of a vertical shaft and by being laminated (Goldring, 1996).

It would be interesting to know to what extent *Pholeus* occurs in similar deposits of different age from the Muschelkalk carbonates. As explained below, *Pholeus* seems to be characteristic of a shallow-marine to lagoonal carbonate environment (intertidal to shallow subtidal) with firmgrounds at omission surfaces (discontinuity surfaces). However, further research will show how much this ichnogenus is also associated with deeper marine environments.

BURROW PRODUCER AND PALEOBIOLOGY

The passively-filled simple burrow structure of *Pholeus* is most easily interpreted as a dwelling structure (domichnion), produced by a tracemaker that lived mainly as a sessile suspension feeder. Producers of similar modern burrows are numerous, but because of their geometry, size, wall lining and especially the diagnostic slender shaft, *Pholeus* is most likely assignable to the activity of

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FIGURE *6*— *1–2*, *Pholeus platiformis* n. isp., holotype, IMPG Gö 1225-5, Wellenkalk-1-Member of quarry Geilsdorf, Thuringia (top and side views). *3–4*, *Pholeus platiformis* n. isp., paratype, IMPG Gö 1225-6, Wellenkalk-1-Member of Jena-Zwätzen, Thuringia (top and bottom views). *5–9*, *Pholeus elongatus* n. isp., holotype, IMPG Gö 1225-8, Wellenkalk-3-Member of quarry Gutendorf, Thuringia; *5*, top view; *6*, branching point of the vertical shaft which is not preserved due to intense emplacement by celestine crystals; *7*, bottom view (part) with secondary burrows of *Archaeonassa fossulata*; *8*, bottom view (part) with a regular system of pellets on both margins; *9*, side view with pellets. *10–11*, *Pholeus elongatus* n. isp., paratypes, IMPG Gö 1225-9 and -10, Wellenkalk-3-Member of quarry Rittersdorf, Thuringia. Scale bar in Fig. *6.5* = 10 cm, all other scale bars = 1 cm.

decapod crustaceans. *Pholeus bifurcatus* burrow system corresponds somewhat with modern burrows produced by crabs, such as the stone crab *Menippe mercenaria* (see Frey et al., 1984) or *Goneplax rhomboids* (Rice and Chapman, 1971). Crabs first appeared in the Lower Jurassic probably with a non-fossorial behaviour, however, discounting crabs as the potential producer of *Pholeus*. On the other hand, the small vertical shaft typical of *Pholeus* agrees quite well with shafts known from thalassinian shrimps such as *Callianassa* sp. (Braithwaite and Talbot, 1972, pl. 2, 3; Bromley, 1996, fig. 4.25) and *Neocallichirus grandimina* (Dworschak and Ott, 1993, fig. 6B, C). The creation of a tube smaller in diameter than the animal itself is not fully understood, but its functions clearly seem to be related to a ventilation system, which enables the inhabitant to flush, aerate and clean its burrow. Other potential candidates include lobsters (e.g., *Homarus* and *Nephrops*) with a mud-dwelling behaviour. The Norway Lobster *Nephrops norvegicus* strongly represents a modern example of *Pholeus*-like burrows (Chapman and Rice, 1971; Rice and Chapman, 1971; Atkinson, 1974). In addition, modern stomatopod burrows, for example *Pseudosquilla* as described by Braithwaite and Talbot (1972), resemble *Pholeus elongatus* in general shape and size, but they lack a vertical shaft.

TRACE FOSSIL TAPHONOMY AND PALEOENVIRONMENTAL IMPLICATIONS

A few typical features of *Pholeus* are worth discussion. First is the occurrence of compound burrow systems as with in *P. abomasoformis*. Although compound burrows seem to belong to one producer (due to similar burrow morphology, size and wall pattern) in most of the studied specimens, they do not appear to have originated by true branching. More likely, they originated either by growth of the tracemaker, as the lower structure is larger than the upper; or by an upward shifting of the tracemaker, which created a new burrow starting at the larger tunnel of the abandoned burrow. A sudden accumulation of sediment resulting from rapid event deposition, wave action, or even tidal currents is probably the cause of that upward migration. In such a case, the infaunal animal would try to compensate for the amount of new sediment by adjusting its burrow upward and abandoning the former one. In response to a sudden sediment incursion of some cm or dm, a new retrusive burrow part would result (escape trace, Fig. 5.7). On the other hand, continuous sedimentation is reflected by gradual burrow shifting to keep pace with seafloor fluctuations and spreiten-like structures result (equilibrium trace, Fig. 5.8). Similar examples are also reported from other trace fossils, e.g. *Diplocraterion* (Goldring, 1962) and *Ophiomorpha* (Hester and Pryor, 1972). Owing to the lack of coarse-grained lithologies and sedimentary structures that indicate a higher flow regime, event deposition may be discounted as a possible reason for retrusive burrow parts. Moreover, the micritic and dolomitic platy limestone hosting some of the compound burrows is characterized by oscillation ripple marks, algal laminations, desiccation cracks and vertebrate footprints. Therefore, it may be concluded that the burrows shifted upwards more likely because of sediment input related to tidal currents.

Another aberration includes burrow parts that differ from the described *Pholeus* burrows in having a circular cross-section with a smaller diameter and fewer pellets on the wall. They do not belong to secondary burrows as described below because they are intersected by some of them and they start from certain burrow ends of the parent burrow. A smaller diameter as well as the imperfect wall lining suggests they may be burrow parts of another, smaller animal. Apart from this, secondary burrows are typically associated with *Pholeus* as already mentioned by Fiege (1944, p. 426). Common associated ichnotaxa that have been recognized include *Archaeonassa fossulata*, *Chondrites* isp. and *Planolites montanus*. *A. fossulata* occurs either as an exogenic trail or as an endogenic burrow as described by Fenton and Fenton (1937). According to Buckman (1994), it is a good indicator for intertidal regimes.

In order to test whether burrows showed any degree of common orientation, some were measured in situ (cf. Hill and Hunter, 1973; Hohenegger and Pervesler, 1985). Only at one horizon was a common orientation clearly indicated. At this locality, the position of the paleoshoreline has been reconstructed, with the burrows oriented perpendicular to the shoreline, the small opening toward land.

Around 60 specimens have been collected stratigraphically, providing an overview of the distribution of described species in the Lower Muschelkalk section. *Pholeus* is more or less restricted to a marly limestone with a cyclic flasery and platy texture. The most widespread occurrence in the whole section is covered by *P. abomasoformis* and *P. bifurcatus*, whereas *P. platiformis* seems to be restricted to the Wellenkalk-1 and 2-Members. *P. elongatus* is reported in the upper part of Wellenkalk-2-Member as well as the Wellenkalk-3-Member (Fig. 2). This stratigraphical distribution might reflect certain evolutionary trends of the burrow-producing animal and may be associated with a phylogenetic increase in size.

The Germanic Basin during the Lower Muschelkalk age is interpreted as a shallow epicontinental sea containing several carbonate platforms (Knaust, 1997). Together with large *Rhizocorallium* spreiten, *Pholeus* seems to be restricted to the shallowest facies, which is characterized by features typical of a shallow-marine to lagoonal environment in an intertidal to shallow subtidal setting. The preferred occurrence of *Pholeus* at erosion structures (e.g., tidal channels) is related to stronger currents, which flush the burrows with aerated water and nutrients. Omission surfaces with firmgrounds give evidence for a certain omission stage between erosion and deposition, at times accompanied by syndepositional deformation (Knaust, 2000), which also may have affected the burrows themselves (Kruck, 1974).

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APPENDIX—List of the studied sites with reference to Table 1 (the historical material from the collection of Göttingen is not included here).

Site	Topographic map (1:25 000)	Coordinates (Gauß-Krüger)
Geilsdorf (GSD)	5232 Stadtilm	R 44 36 600, H 56 23 400
Rittersdorf (RD)	5133 Kranichfeld	R 44 45 400, H 56 32 700
Gutendorf (GD)	5033 Weimar	R 44 45 000, H 56 42 400
Tannroda-Böttelborn (BB)	5133 Kranichfeld	R 44 47 600, H 56 34 800
Teichel (TC)	5133 Kranichfeld	R 44 51 700, H 56 29 600
Saalborn (SB)	5133 Kranichfeld	R 44 52 760, H 56 40 100
Hohenfelden (HF)	5132 Marlishausen	R 44 40 010, H 56 39 800
Jena-Zwätzen (JZ)	5035 Jena	R 44 71 450, H 56 47 010
Lengefeld (LGF)	5134 Blankenhain	R 44 56 200, H 56 32 250