THE AMMONITE *SUTNERIA* FROM THE UPPER JURASSIC OF SOUTHERN SPAIN

by F. OLÓRIZ *and* F. J. RODRÍGUEZ-TOVAR

ABSTRACT. A bed-by-bed collection of 144 specimens of the ammonite genus *Sutneria* from the uppermost Oxfordian and lowermost Kimmeridgian of southern Spain comprises the species and subspecies *galar* Oppel, *galar thieli* Zeiss, *nusplingensis* Fischer and *platynota* Reinecke. These represent the most complete assemblage of the genus known from the western Tethys. All the species, except *nusplingensis*, were found in epicontinental facies (alternating marls, marly limestones and limestones) as well as in epioceanic facies (*ammonitico rosso*). *S. nusplingensis* occurs only rarely at the base of the epicontinental Kimmeridgian. *S. galar thieli* ranges from the upper Planula Zone of the Upper Oxfordian to the Platynota Zone of the Lower Kimmeridgian. *S. galar* and *S. platynota*, by far the most common species, show their normal stratigraphical distribution in the uppermost Oxfordian and lower Kimmeridgian, respectively; this reinforces their usefulness for correlation in the European Tethys and surrounding areas.

THE genus *Sutneria* Zittel, 1884 comprises small ammonites normally included in the subfamily Aulacostephaninae Spath, 1924 (e.g. Arkell *et al.* 1957; Barthel 1959; Geyer 1961; Schairer 1970; Contini and Hantzpergue 1975), although classification at this systematic level is still open to discussion (Berckhemer and Hölder 1959; Olóriz 1978; Zeiss 1979; Callomon *in* Donovan *et al.* 1981). These ammonites develop bifurcate, polygyrate and even fasciculate ribbing on their planulate or globose shells, and only rarely exhibit tubercles. In the uppermost Kimmeridgian and Lower Tithonian, only slightly ornamented or almost smooth forms are known. In Submediterranean Europe and on the northern margin of the westernmost Tethys, *S. galar* (Oppel) and *S. platynota* (Reinecke) are valuable biostratigraphical markers characterizing, respectively, the youngest subzone of the Oxfordian and the oldest zone of the Kimmeridgian. Previously, these two species have been recognized most often in Submediterranean ammonite assemblages, with less well documented records from more southerly regions. In the Iberian Peninsula (Text-fig. 1), outside the Betic Cordillera, one or both of these species have been found in the Iberian Chain (Geyer 1966, 1969; Meléndez *et al.* 1983, 1990; Moliner 1983; Atrops and Meléndez 1984; Moliner and Olóriz 1984) and in Portugal (Marques 1983; Atrops and Marques 1986, 1988; Rodríguez-Tovar 1993). In the Betic Cordillera, *S. platynota* (Reinecke) and/or *S. galar* (Oppel) have been cited by Behmel (1970), Fourcade (1970, 1971), Azéma *et al.* (1971), López-Garrido (1971), Azéma (1977), Olóriz (1978, 1979), Sequeiros and Olóriz (1979), García-Hernández *et al.* (1979, 1981), Rodríguez-Tovar (1990, 1993), Olóriz *et al.* (1991, 1992), López-Galindo *et al.* (1992) and Olóriz and Rodríguez-Tovar (1993*a*, 1993*b*). Although the genus has been known in southern Spain for many years, only the recent papers of the present authors established its moderate abundance in the uppermost Oxfordian and lowermost Kimmeridgian, and recent research has extended the biogeographical range of the more common species.

SECTIONS STUDIED AND STRATIGRAPHICAL REMARKS

A total of 142 specimens of *Sutneria* was collected by the authors from nine sections in southern Spain (Text-fig. 1). These are Fuenta Alamo (FA) (sheet 26–32, Montealegre del Castillo: 1°25′20″ W, 38°41′45″ N), Elche-Férez (EF) (sheet 24–34, Elche de la Sierra: 2°00′10″ W,

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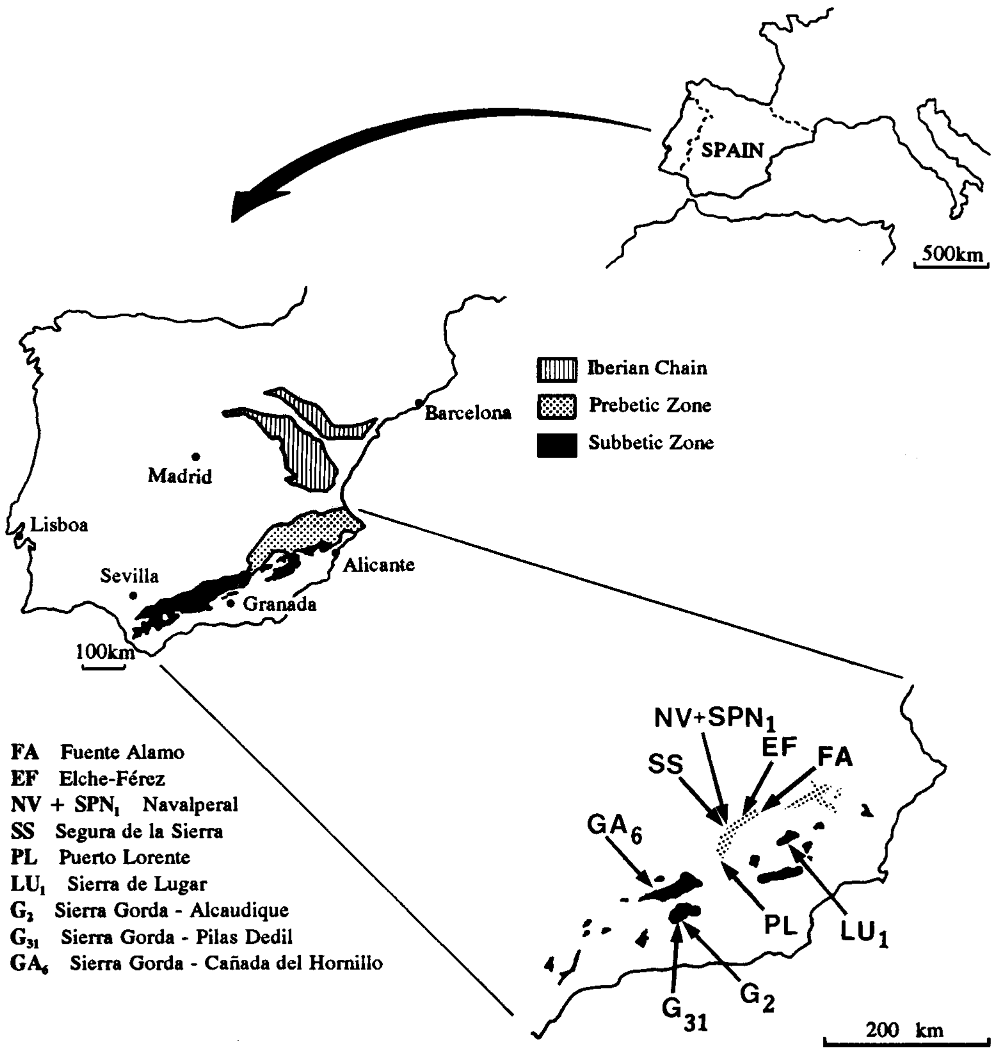
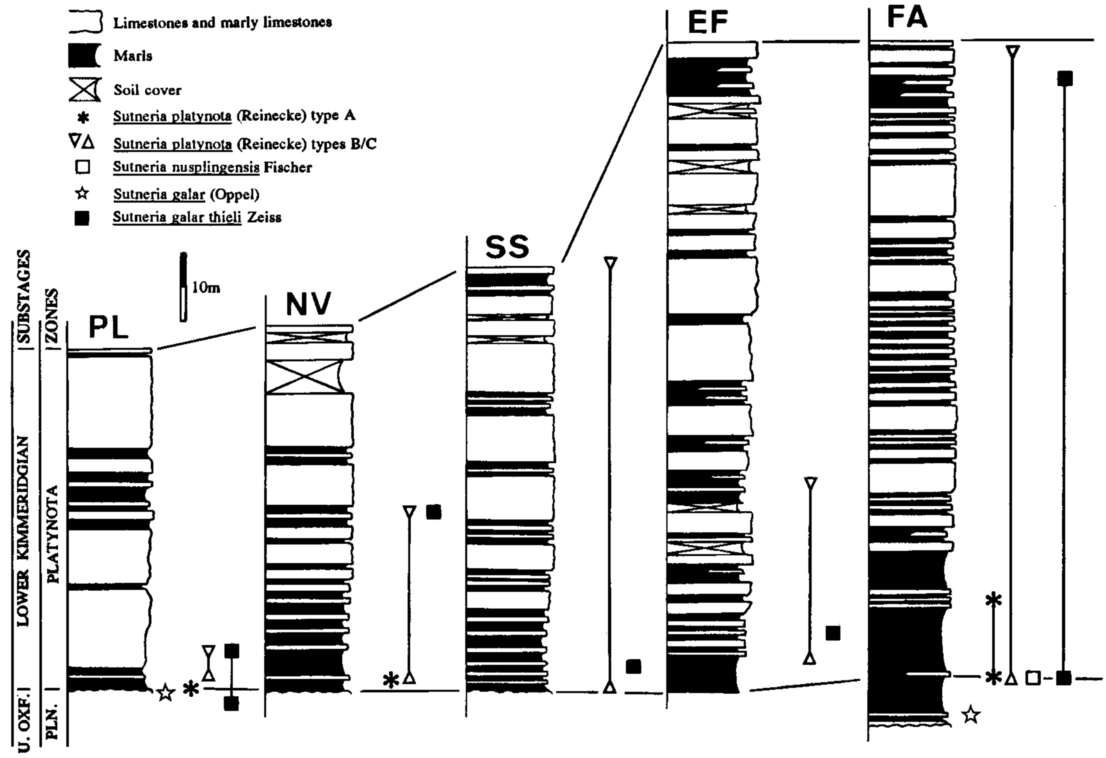
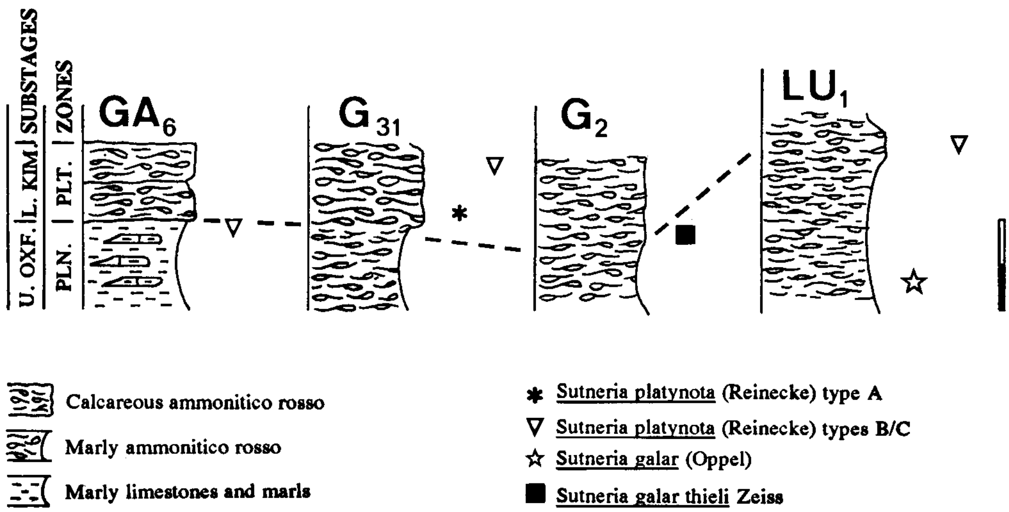


TEXT-FIG. 1. Upper Jurassic outcrops in southern Spain. Subbetic Zone (black), Prebetic Zone (stippled). Sections: Sierra Gorda-Alcaudique (G_2), Sierra Gorda-Pilas Dedil (G_{31}), Sierra Gaena-Cañada del Hornillo (GA_6), Sierra de Lugar (LU_1), Puerto-Lorente (PL), Segura de la Sierra (SS), Navalperal (NV and SPN_1), Elche-Férez (EF), Fuente Alamo (FA).

38°23′20″ N), Navalperal (NV) and (SPN_1) (sheet 22–35, Orcera: 2°37′00″ W, 38°18′30″ N), Segura de la Sierra (SS) (sheet 22–35, Orcera: 2°38′25″ W, 38°18′05″ N), Puerto Lorente (PL) (sheet 21–37, Cazorla: 2°59′25″ W, 37°50′15″ N), Sierra Gorda-Alcaudique (G_2) (sheet 18–42, Loja: 4°8′25″ W, 37°7′53″ N), Sierra Gorda-Pilas Dedil (G_{31}) (sheet 18–42, Loja: 4°3′13″ W, 37°2′57″ N), Sierra de Gaena-Cañada del Hornillo (GA_6) (sheet 17–40, Lucena: 4°18′48″ W, 37°25′20″ N), and Sierra de Lugar (LU_1) (sheet 27–35, Fortuna: 1°10′45″ W, 38°12′49″ N). Sheet numbers refer to the 1:50000 topographical series. In addition, two specimens of *S. platynota* (Reinecke) were collected from the lower part of two other sections with poorly exposed or ammonite-poor Kimmeridgian strata. This collection of 144 specimens is by far the most complete *Sutneria* assemblage known from the uppermost Oxfordian and the lowermost Kimmeridgian in the western Tethys.



TEXT-FIG. 2. Lithologies, ammonite distribution and stratigraphy of the studied sections in epicontinental areas.



TEXT-FIG. 3. Lithologies, ammonite distribution and stratigraphy of the studied sections in epioceanic areas. Scale bar represents 0·2 m.

Text-figures 2–3 show the stratigraphical distribution of species in the sections analysed. It is noteworthy that *S. platynota* was recorded in two relatively close but extremely different eco-sedimentary environments having, for example, enormous thickness differences for equivalent bio-chronostratigraphical intervals. In the epicontinental Prebetic (sections PL, SS, NV, EF and FA), comparatively extended successions of the Puerto Lorente Formation (Pendas 1971) mainly comprise alternating limestones and marls, and are relatively poor in ammonites. Differences in *Sutneria* records obtained in these areas are not clearly related to lithology. In the epioceanic Subbetic (sections G_2, G_{31}, GA_6 and LU_1), ammonite-rich nodular limestones belonging to the Ammonitico Rosso Superior Formation (Molina 1987) show comparatively extreme stratigraphical condensation, and represent the typical deposits in distal pelagic swells in the Tethys.

SYSTEMATIC PALAEONTOLOGY

Location of specimens. All the specimens studied are in the collections of the Departamento de Estratigrafía y Paleontología of the University of Granada (Spain) with catalogue numbers prefixed PL, SS, SPN, RG-CH, BU, FA, EF, FLU, FG, FGA, and ZG.

Conventions. Dimensions are given in millimetres for only those specimens for which complete measurements were possible. Dm = maximum diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; U/D = umbilicus:shell diameter ratio; Wb/D = whorl breadth:shell diameter ratio; FTD = diameter at the first external tubercle; LTD = diameter at the last external tubercle; UR/2 = number of umbilical ribs per half whorl; VR/2 = number of ventral ribs per half whorl; T = number of external tubercles; PLTUR = number of umbilical ribs after the last external tubercle; RI = rib index or the number of ventral ribs per ten umbilical ribs.

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily PERISPHINCTACEAE Steinmann *in* Steinmann and Doderlein, 1890
Family AULACOSTEPHANIDAE Spath, 1924
Subfamily AULACOSTEPHANINAE Spath, 1924

Genus SUTNERIA Zittel, 1884

Type species. Nautilus platynotus Reinecke, 1818. Neotype, from Ützing, North Franconia, Germany, designated by Geyer (1961 p. 131, pl. 3, fig. 11).

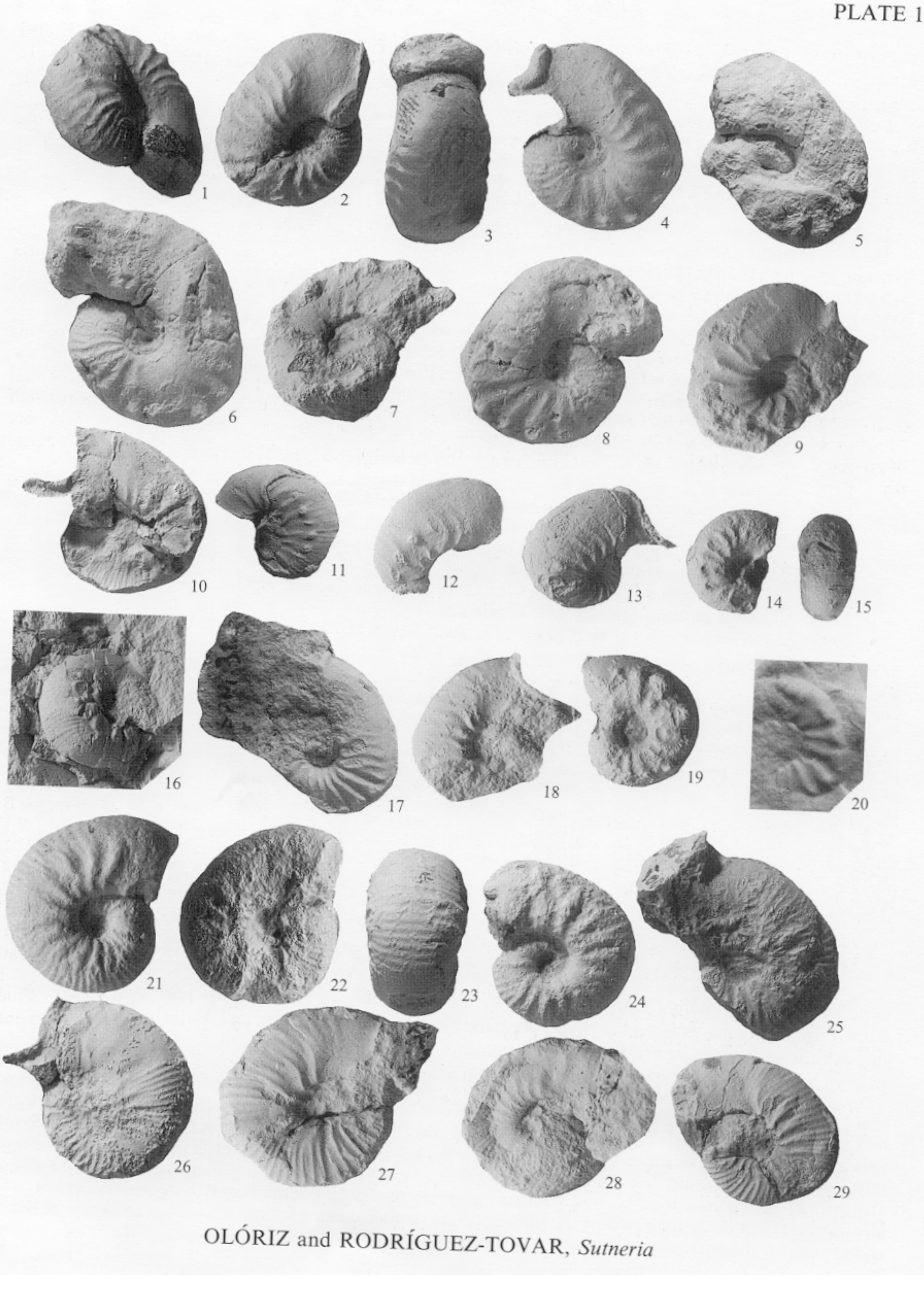
EXPLANATION OF PLATE 1

Figs 1–20. *Sutneria platynota* (Reinecke, 1818); microconchs; Platynota Zone. 1–2, F.LU_1.G.2; morphotype B; Sierra de Lugar; Bed G. 3–4, F.LU_1.G.3; morphotype C; Sierra de Lugar; Bed G. 5, F.GA_6/7.1; morphotype B/C; Sierra de Gaena-Cañada del Hornillo; boundary between Beds 6 and 7. 6, F.LU_1.G.1; morphotype B/C; Sierra de Lugar; Bed G. 7, NV-o.1; morphotype A; Navalperal; Bed O. 8, F.LU_1G.4; morphotype B/C; Sierra de Lugar; Bed G. 9, FA-75.59; morphotype A/B; Fuente Alamo; Bed 75. 10, SS-(30)19A.1; morphotype B; Segura de la Sierra; 0·3 m below Bed 19A. 11, SPN_1-33.2; morphotype C; Navalperal; Bed 33. 12, EF-6.1; morphotype B; Elche-Ferez; Bed 6. 13, SS-4.9; morphotype B/C; Segura de la Sierra; Bed 4. 14–15, PL-HG.C.3; morphotype A; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 16, FA-6.90; morphotype A; Fuente Alamo; Bed 6. 17–18, SPN_1-31.6; morphotype C; Navalperal; Bed 31. 19, PL-HG.C.2; morphotype A; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 20, FA-53.1; Fuente Alamo; Bed 53.

Figs 21–29. *Sutneria galar* (Oppel, 1863); microconchs; Planula Zone (Galar Subzone). 21, München AS VIII 34; original (cast) figured by Oppel (1863, pl. 67, fig. 5) and designated lectotype by Barthel (1959, p. 59, pl. 6, figs 8–9); Thalmässing (Mfr.); 'Weisser Jura β_2, 22, F.LU_1.G(30–35).1; Sierra de Lugar; 0·3–0·35 m below Bed G. 23–24, PL-HG.C.1; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 25, PL-HG.C.100; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. 26, FA-4.201; Fuente Alamo; Bed 4. 27, FA-4.19; Fuente Alamo; Bed 4. 28, FA-4.201; Fuente Alamo; Bed 4. 29, FA-4.237; Fuente Alamo; Bed 4.

Bed numbers follow Olóriz (1978) and Rodríguez-Tovar (1993).

All × 1·5.



OLÓRIZ and RODRÍGUEZ-TOVAR, *Sutneria*

Sutneria platynota (Reinecke, 1818)

Plate 1, figures 1–20; Text-figure 4

1818 *Nautilus platynotus* Reinecke, p. 72, pl. 4, figs 41–42.
1877 *Ammonites* (*Perisphinctes*) *platynotus*, Reinecke; Favre, p. 47, pl. 5, fig. 2.
1878 *Ammonites* (*Perisphinctes*) *platynotus*, Reinecke; de Loriol, p. 91, pl. 15, figs 1–2.
non 1878 *Perisphinctes platynotus* Reinecke; Herbich, p. 166, pl. 11, fig. 2.
1886 *Ammonites platynotus* (Reinecke); Pillet, p. 10, pl. 1, figs 9–12.
1887–88 *Ammonites platynotus* Reinecke; Quenstedt, p. 999, pl. 112, fig. 6.
1887–88 *Ammonites reineckianus* Quenstedt, p. 1001, pl. 112, figs 7–14, 18 (?15, *non* 16–17); p. 1020, pl. 116, fig. 14.
1961 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Geyer, p. 131, pl. 3, figs 11–12.
1964 *Sutneria platynota* (Rein.); Hölder, p. 242, fig. 73–3.
1969 *Sutneria platynota* (Reinecke); Geyer, p. 65, fig. 1.
1970 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Schairer, p. 155, pl. 1, figs 1–12; pl. 2, figs 1–13.
1974 *Sutneria* (*Sutneria*) *platynota* (Reinecke); Nitzopoulos, p. 81, pl. 9, fig. 14.
1975 *Sutneria*; Ziegler, pl. 5, fig. 1
1977 *Sutneria platynota* (Reinecke); Ziegler, p. 21, pl. 3, fig. 3.
1978 *Sutneria platynota* (Reinecke); Olóriz, p. 371, pl. 39, fig. 2.
1982 *Sutneria platynota* (Reinecke); Atrops and Benest, p. 952, pl. 1, figs 4–6.
1986 *Sutneria platynota* (Reinecke); Atrops and Marques, p. 541, pl. 1, figs 4–5.
1990 *Sutneria platynota* (Reinecke); Bennetti *et al.* p. 34, fig. 2.
?1990 *Sutneria* sp. juv. cf. *platynota* (Reinecke); Bennetti *et al.* p. 34, pl. 1, figs 14–15.
1991 *Sutneria platynota* (Reinecke); Cope, p. 329, pl. 4, figs 3, 5–6.
1992 *Sutneria platynota*; Finkel, p. 246, fig. 83.
1993*a* *Sutneria platynota* (Reinecke); Olóriz and Rodríguez-Tovar, p. 93, figs 2–3.
1993*b* *Sutneria platynota* (Reinecke); Olóriz and Rodríguez-Tovar, p. 160, fig. 4c.
1993 *Sutneria platynota* (Reinecke); Rodgríguez-Tovar, p. 220, pl. 6, figs 2–4.

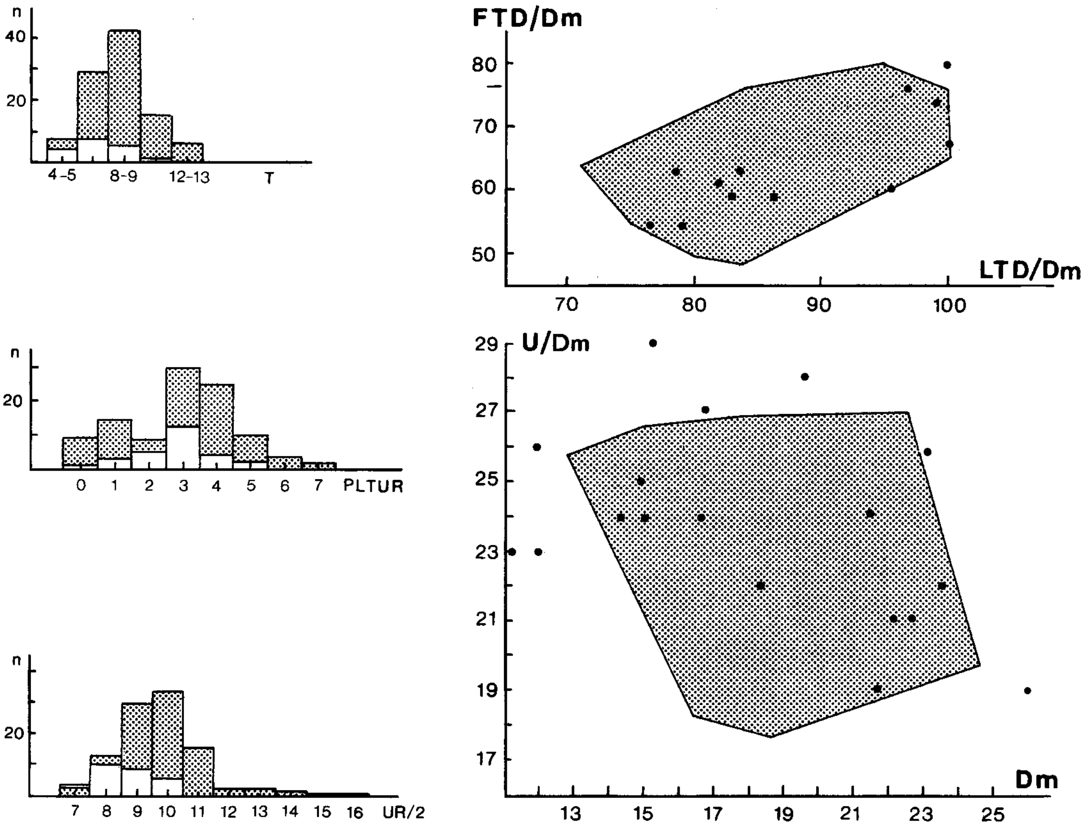
Material. Seventy-three specimens, many of which are crushed.

Dimensions.

	Dm	U	U/D	UR/2	T	FTD	LTD	PLTUR
PL-HG.C.2	16·6	4	0·24	8	8	9·9	15·8	1
PL-HG.C.3	12	3·1	0·26	10	7	9·1	11·5	1
SS-4.9	15	3·8	0·25	8	6	9·5	11·7	4
SS-6.19	11	2·5	0·23	8	7	—	10·5	⩾ 2
SS-6.38	15	3·6	0·24	7	6?	≈ 12	15	—
SS-10.36	12	2·7	0·23	8–9	4	8·9	11·9	—
SS-19.A	19·7	5·5	0·28	≈ 8	5?	12·5	16·4	3
NV-0.I	23·1	5·9	0·26	—	6	15·7	23·1	0
EF-6.1	16·6	4·6	0·28	7–8	3?	—	—	2
FA-53.1	15·3	4·3	0·29	9	⩾ 6	—	14·5	—
FA-75.59	18·3	4	0·22	6–7	⩾ 4	—	14·6	2–3

Diagnosis. Small, involute ammonites with rounded whorls and external tubercles on the last whorl. Ribs bifurcate and polygyrate with occasional ventral intercalatories. Variable pre-peristomal smoothing and whorl contraction. Pendunculate peristome.

Description. Measured specimens range from 11 to 26 mm in size. Coiling is moderately involute (19–29 per cent.). Whorl section is subrounded with broad venter. Rib density varies depending on the presence of tubercles on the last whorl. The number of umbilical ribs per half whorl is 6–10 on the outer whorl. The first appearance of external tubercles varies (FTD/Dm = 0·54–0·76), and the last tubercle is seen at 76–90 per cent. of the maximum diameter. The external tubercles are more or less well developed and numerous (> 3–11), as are the pre-peristomal primary ribs without tubercles (0–5). Five ornamental ontogenetic phases were identified: (1), on the hidden part of the phragmocone (before the last whorl), ribs range from fine to dense, and are coarse and widely spaced; division points are on the inner flanks, secondaries pass the venter without



TEXT-FIG. 4. Shell morphology of *Sutneria platynota*. Stipple represents data from southern Germany based on Schairer (1970). White areas in bars (left) and black spots (right) represent specimens from southern Spain. n = number of specimens. See text for abbreviations of shell characters.

modification and there are intercalatories; (2), rib density decreases progressively but the ribs are slightly more sinuous, divisions are higher on the flanks and secondaries are more separated; (3), primary ribs are reinforced with very small and slight radial thickening of their outer extremities to which two ventral ribs generally connect; (4), very typical strengthening of primaries which widen upwards on the flanks to connect with well-developed rounded or tangentially elongated tubercles and three ventral ribs; the progressive weakening of ventral ribs typically determines the smoothing of the venter; and (5), final developmental phase lacks external tubercles, and has a variable development of umbilical, and more or less sinuous, ribs; unsculptured shell precedes the peristome, which is pedunculate and generally with long, pointed lappets and ventral collar.

Remarks. The existence of external tubercles clearly differentiates this species from other *Sutneria*. The recognition of morphotypes ('Formengruppe'), first demonstrated by Schairer (1970) and then observed by Atrops and Benest (1982), Moliner (1983), Rodríguez-Tovar (1990) and Olóriz and Rodríguez-Tovar (1993*a*, 1993*b*) in epicontinental deposits in North Africa and Iberia, is significant but only 40 of our specimens are well enough preserved to recognize them. Incomplete preservation of the pre-peristomal part of the shell at times limited their precise identification, but we recognized seven morphotype A, nine morphotype B and three morphotype C specimens. Specimens transitional between morphotypes A and B (six) and morphotypes B and C (15) were found in both epicontinental and epioceanic (*ammonitico rosso*) facies. This must be of significance because the stratigraphical distribution of morphotypes in southern Spain is not as well differentiated as that recognized in southern Germany (Schairer 1970). In southern Spain, morphotype A specimens were recorded in the lowermost part of the sections studied, but the other morphotypes have a wide stratigraphical distribution within the Platynota Zone. The relative abundance of Schairer's morphotypes also seems to differ from that in southern Germany. According to Schairer (1970), morphotype A and morphotype B are more abundant in the Frankischen Alb. In southern Spain, morphotype B, morphotype C and forms intermediate between them are much more common. This cannot be fully explained at present, but morphotype B and morphotype C specimens are also more common against figured specimens from other localities outside Germany. Some other differences affect shell structure and sculpture. As shown in Text-figure 4, the assemblage from southern Spain fits comfortably within the lower range in number of umbilical ribs per half whorl, number of external tubercles, and number of primary ribs after the last external tubercle as determined for southern German populations (Schairer 1970); coiling values indicate some smaller and more evolute specimens in southern Spain. On the other hand, the relative first and last appearance of external tubercles is comparable in the two regions.

Occurrence. In Europe, *Sutneria platynota* is typically found in the basal beds of the Submediterranean Kimmeridgian. According to Hantzpergue (1989), this species has not been recorded in Normandy, and is unknown in England. It is rare in Africa, with scarce records from western Algeria (Atrops and Benest 1982, 1984) and no records from the Moroccan internal Prerif (Benzaggagh 1988) and eastern Africa (Zeiss 1979, 1984). The record of six specimens of the species in northern Anatolia (Aktas Bünüs, e.g. Cope 1991) is noteworthy. Marques (1983) found rare specimens in the Algarve (southern Portugal), a record comparable to that of the nearby Betic Cordillera (Rodríguez-Tovar 1993; Olóriz *et al.* 1994). On the basis of our collection, a moderate frequency of occurrence must be considered for this species in the epicontinental Kimmeridgian in southern Spain. In the Mediterranean epioceanic Subbetic, *S. platynota* is less common, and very rare further east in the same facies (western Lessinian Alps, e.g. Benetti *et al.* 1990). Outside the Mediterranean Tethys, Burckhardt (1930) cited *S.* aff. *platynota* from the Barranca del rio Vinasco in the Huasteca (east Mexico), but it was not figured and never collected again. During research in progress, one of us (F. Olóriz) failed to find the species in the Mexican Altiplano, or in the Burckhardt type section in the Huasteca (Veracruz, Mexico).

Sutneria galar (Oppel, 1863)

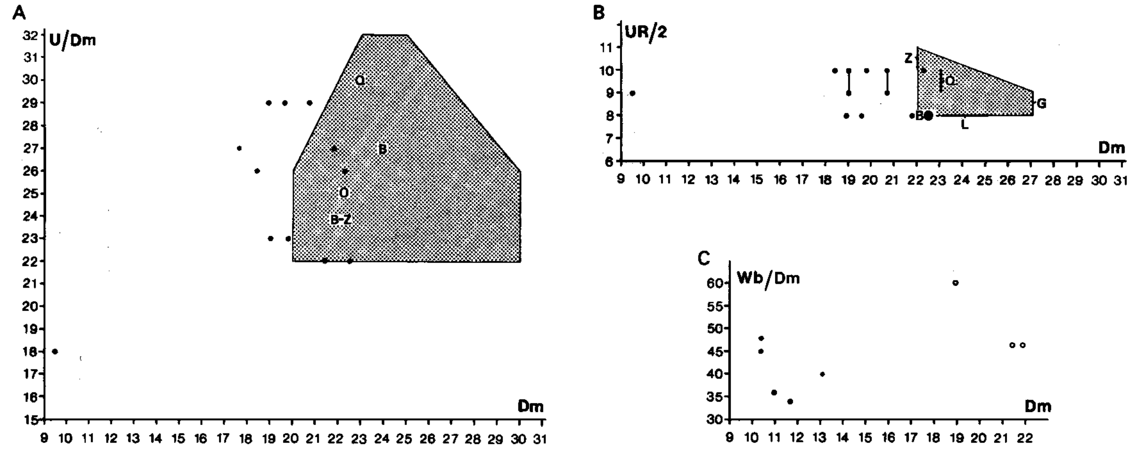
Plate 1, figures 21–29; Text-figures 5, 6A–E

1863 *Ammonites galar* Oppel, p. 234, pl. 67, fig. 5.
1878 *Ammonites* (*Perisphinctes*) *galar*, Oppel; de Loriol, p. 90, pl. 15, fig. 5.
1879 *Perisphinctes galar*, Oppel; Fontannes, p. 75, pl. 11, fig. 5.
?1887–88 *Ammonites reineckianus* Quenstedt, p. 1002, pl. 112, fig. 17.
1959 *Sutneria galar* (Oppel); Barthel, p. 59, pl. 6, figs 8–10.
1961 *Sutneria* (*Sutneria*) *galar* (Oppel); Geyer (*partim*), p. 132, pl. 4, fig. 7.
1964 *Sutneria galar* (Opp.); Hölder, p. 242, fig. 73–2.
1969 *Sutneria galar* (Opp.); Barbulescu, pl. 2, figs 1–10.
1969 *Sutneria galar* (Oppel); Geyer, p. 65, fig. 1.
1977 *Sutneria galar* (Oppel); Ziegler, p. 19, pl. 2, fig. 3.

Material. Fifty-four specimens, commonly crushed except in condensed limestones.

Dimensions.

	Dm	U	U/D	UR/2	VR/2	RI	Wb	Wb/D
PL-Oxf.C.1	18·9	5·5	0·29	8	26	30	11·4	0·6
PL-HG.C.100	21·8	5·8	0·27	8?	≈ 28	—	10	0·46
FA-Oxf	9·5	1·7	0·18	9	22?	—	—	—
FA-4.19	22·5	5	0·22	8	27	33	—	—
FA-4.200	19·8	4·5	0·23	≈ 10	≈ 30	≈ 30	—	—
FA-4.201	20·7	5·9	0·29	9–10	31	≈ 28	—	—
FA-4.202	22·3	5·7	0·26	≈ 10	≈ 32	≈ 32	—	—
FA-4.203	17·6	4·8	0·27	—	—	—	—	—
FA-4.219	18·4	4·7	0·26	10	29	29	—	—
FA-4.229	19	4·3	0·23	9–10	> 26	> 26	—	—
FA-4.237	19·6	5·7	0·29	8	27	32	—	—
FLU_1.G (30–35).1	21·4	4·8	0·22	—	—	—	9·9	0·46



TEXT-FIG. 5. Shell morphology of *Sutneria galar* (Oppel) and *S. g. thieli* Zeiss. See text for abbreviations of shell characters. Black spots/circles represent Spanish specimens. A–B, stippled area represents populations from southern Germany and northern Switzerland. Data for *Sutneria galar* (Oppel) based on de Loriol (1878) and Geyer (1961); letters B, L, G, O, Q, and Z represent specimens figured respectively by Barthel (1959), de Loriol (1878), Geyer (1961), Oppel (1863), Quenstedt (1887–88) and Ziegler (1977). C, black circles represent *S. galar* (Oppel); black spots represent *S. g. thieli* Zeiss.

Diagnosis. Small and relatively involute ammonites with subrounded whorl section and broad venter. Bifurcate, polygyrate-fasciculate and intercalatory ribs on last whorl. Reduced pre-peristomal smoothing and whorl contraction. Pedunculate peristome.

Description. In the best-preserved 12 specimens, of 20 measured, size ranged from 9·5 to 22·5 mm. Coiling is moderately involute (18–29 per cent). The outer whorl is sometimes irregularly, rather than concentrically, coiled. Whorl thickness, measurable in only three specimens, is 46–60 per cent. Ribbing density fluctuates especially on the phragmocone, where ribs are mainly bifurcate with some intercalatories, but clearly decreases on the last half whorl. Towards the end of the phragmocone and on the body chamber, umbilical ribs become progressively stronger, and polygyrates and/or intercalatories increase in number. The ribs divide around mid-flank or just below. Primary ribs are slightly sinuous towards the end of the shell or before, if polygyrate ribbing appears early and is well-developed. In the latter case, more falcoid ribbing appears. Rib division very low on the flank was found near the end of the body chamber only in the smallest (?juvenile) specimen. Amongst our specimens, two morphologies were identified according to rib density and coarseness. Pre-peristomal smoothing affects first the ventral and then the primary ribs; the unsculptured shell is only 20–25 per cent. of the last whorl. The shell is less contracted at its end. Lappets are of moderate length, narrow and pointed, with a more or less distinct collar on the ventral side.

Remarks. The absence of tuberculation clearly distinguishes this species from *S. platynota*. Stratigraphical occurrence has been traditionally used to distinguish *S. galar* from other younger species such as *S. cyclodorsata* (Moesch), which is smaller, and develops more sinuous ribs and greater pre-peristomal smoothing. According to Zeiss (1979), *S. galar thieli* Zeiss is a form intermediate between *galar* and *cyclodorsata* in the lowermost Kimmeridgian. The slightly older *S. praecursor* Dieterich shows coarser, simple ribbing. This early species is rightly accepted as the ancestral form of *S. galar*. The presence of only one polygyrate rib in *S. praecursor* (recognizable on the last preserved rib in a cast of Dieterich's original; Dieterich 1940, pl. 1, fig. 2), the coarse and less densely ribbed morphotype in our own collection (similar to that figured in Quenstedt 1887–88, pl. 112, fig. 17), and the record of *Sutneria* ex gr. *galar* (Oppel) from the same horizons in the

Celtiberic range (Moscardón, Teruel, cf. Meléndez *et al.* 1983), support the hypothetical close phylogenetic relationship between *S. praecursor* and *S. galar*. Coiling values and the number of primaries per half whorl in our specimens were compared with those obtained from casts and figures of conspecific specimens mainly from southern Germany and northern Switzerland (see synonymy list above). Text-figure 5 shows comparable coiling and rib densities in the two assemblages analysed, even though the specimens from southern Spain are slightly smaller.

Occurrence. *S. galar* characterizes the uppermost Oxfordian, upper Planula Zone (Galar Subzone) in Submediterranean Europe. It has also been recorded in north-west France (Charentes, cf. Hantzpergue 1989) but not in England. In southern Submediterranean areas, like epicontinental Iberia and North Africa, *S. galar* has generally been considered to be scarce or very rare; data presented by Marques (1983, 1984), and Atrops and Marques (1986) indicate similar rarity in Portugal. Atrops and Meléndez (1984) and Meléndez *et al.* (1990) provided similar data for the north-eastern Iberian chain, but more common occurrences of *S. galar*, and/or related forms, were reported by Meléndez *et al.* (1983) from Moscardón (Teruel), a more southerly section in the Iberian Chain. In southern Spain, *S. galar*, as well as *S. praecursor*, have been identified in the Prebetic (García-Hernández *et al.* 1979, 1981; Olóriz *et al.* 1992; Olóriz and Rodríguez-Tovar 1993*a*, 1993*b*). Careful sampling in North Africa, has enabled recognition of the uppermost Oxfordian Planula Zone; specimens include *S. praecursor*, only from Algeria (Atrops and Benest 1984), but *S. galar* was not recorded. On the other hand, *S. galar* and related forms are known from epicontinental deposits in eastern Africa (Somalia, e.g. Spath 1935, and Ethiopia, e.g. Zeiss 1979, 1984). In the Mediterranean Tethys *sensu stricto*, *S. galar* has been reported locally from the Subbetic and its correlative in southern Spain (Sequeiros and Olóriz 1979; Comas *et al.* 1981), and also from Italy (Wendt 1971; Benetti *et al.* 1990), where *Sutneria* is considered to be rare (Sarti 1988). It is known rarely in Sicily (the lower occurrences of *Sutneria cyclodorsata* (Moesch) recorded by Wendt (1971)), and in Romania, *S. galar* has been recognized in the central Dobrogea (Barbulescu 1969) and in the Transylvanian nappes (Bicaz gorges-lacul Rosu area, e.g. Preda *in* Avram 1988).

Sutneria nusplingensis Fischer, 1913

Text-figure 6U

1887–88 *Ammonites reineckianus* Quenstedt, p. 1002, pl. 112, fig. 16.
1913 *Sutneria nusplingensis* n. sp. Fischer, p. 54, pl. 5, fig. 23.

Material. Only one crushed and incomplete specimen with preserved body chamber.

Diagnosis. Small ammonites with rounded whorls, moderate umbilicus and rather complex ribbing on body chamber. Pre-peristomal smoothing. No external tubercles. Pedunculate peristome.

Description. Minimum size is at least *c*. 23–24 mm. Primary ribs are slightly arched, prorsiradiate and clearly strengthened. Secondaries are finer, numerous (24–26 per six primary ribs) and progressively weaker towards the peristome. In the early part of the preserved body chamber, ribbing is mainly bifurcate with intercalatories, but polygyrate and/or fasciculate ribs seem to develop with increased smoothing towards the peristome, which is not preserved.

Remarks. Very rare and not well known, this is a relatively large species with uncomplicated ornament as in other early *Sutneria*. We consider the ribbing variability to be similar to that found in *S. galar* (see above). Fischer (1913) distinguished *S. nusplingensis* from *S. galar* on the basis of larger size, more regular coiling, and less contraction of the body chamber but he admitted a closer morphological relationship with the Kimmeridgian *S. cyclodorsata*, probably for stratigraphical reasons. If our interpretation is correct, *S. nusplingensis* would include relatively large *Sutneria* of the *galar–cyclodorsata* type, which occur rarely in the lowermost Kimmeridgian.

Occurrence. *S. nusplingensis* is known in the Lower Kimmeridgian (Platynota Zone) of southern Spain, southern Germany and northern Switzerland but it has rarely been cited since 1913, when Fischer described one specimen from the 'Weiss-Jura γ' at Nusplingen (Swabian Alb). Geyer (1961) considered *S. nusplingensis* to be synonymous with *S. galar*, and the same as the specimen of *Ammonites reineckianus* figured by Quenstedt

(1887–88, pl. 112, fig. 16), which came from the same area and was the same age as Fischer's material. The range of *S. galar* should therefore extend up into the lowermost Kimmeridgian (lowermost part of the 'Badenerschichten' in the 'Aargauer Jura' of northern Switzerland, cf. Geyer 1961, pp. 132, 140), although the latter author restricted it to the uppermost Oxfordian in southern Germany (cf. Geyer 1961, p. 135). It is significant that *Sutneria* without external tubercles occurs in the Platynota Zone of both southern Germany and southern Spain. As recorded in the Fuente Alamo section, *S. nusplingensis* is found in the lowermost Kimmeridgian of the epicontinental deposits of the eastern Prebetic. Research in progress appears to indicate the presence of this species in western epicontinental areas of southern Iberia (Algarve, Portugal).

Sutneria galar thieli Zeiss, 1979

Text-figures 5, 6F–T

1979 *Sutneria galar thieli* n. subsp. Zeiss, p. 274, pl. 3, fig. 21.

Material. Sixteen almost complete specimens, 14 of which show the body chamber. Crushing is usual except for those specimens collected from nodular limestones.

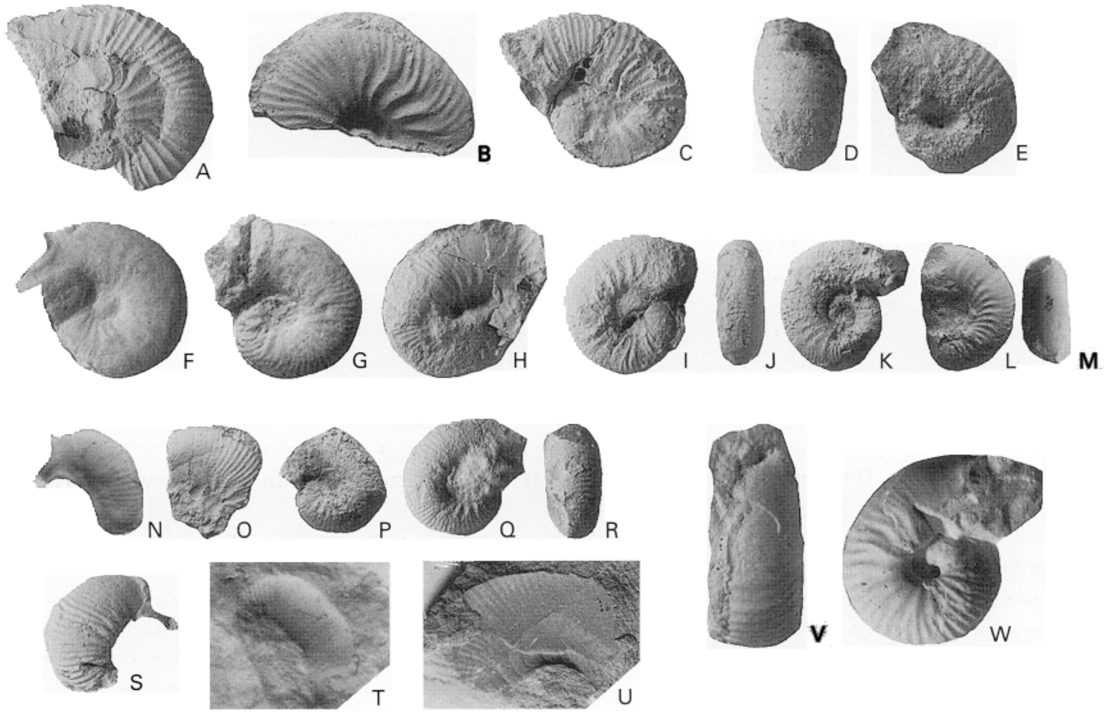
Dimensions.

	Dm	U	U/D	UR/2	VR/2	RI	Wb	Wb/D
PL-HG.C.103	10·7	3	0·28	9	≈ 22	—	—	—
	9·2	2·5	0·27	8–9	—	—	—	—
PL-Oxf.A-1	10·4	2·8	0·27	9	≈ 30	3·4	4·7	0·45
SPN_1.27.184	13·1	3·9	0·30	10	21	21	5·3	0·40
	10·9	3·2	0·29	≈ 11	29	26	—	—
SPN_1.24.120	11	2·9	0·26	15	—	18	4	0·36
	9·2	2·7	0·29	—	—	—	—	—
$Z.G_2$.5b	11·7	3·7	0·32	—	—	—	4	0·34
ZGR.47	10·4	2·4	0·23	10	24	—	5	0·48

Diagnosis. Small ammonites with subrounded–suboval whorls, moderate umbilicus, and bifurcate–polygyrate ribs. Pre-peristomal smoothing and pedunculate peristome.

Description. Sizes range from 10·4 to 13·6 mm. Coiling is moderate (23–32 per cent.), and the whorl section is subrounded or slightly oval, with a more or less broad venter. Periumbilical ribs are more or less strengthened on the body chamber, but generally indistinguishable from secondaries on the phragmocone. Ribs divide around the middle of the flanks or slightly below. Bifurcate ribs with intercalatories are dominant on the outer whorl, and polygyrates may also occur. The sinuosity of ribs and rib density is variable with UR/2 usually around 9–11, and extreme values of 7–15 on the outer whorl. Pre-peristomal smoothing first affects the peripheral sculpture and then progresses to the inner flanks. There is a slight contraction of the anterior body chamber. Thirteen specimens show the peristome, with sword-shaped ('schwertförmige') lappets, or pre-peristomal constriction and small ventral collar.

Remarks. Zeiss (1979) described *S. galar thieli* as a comparatively small subspecies found in the Lower Kimmeridgian (Platynota Zone), with variable ribbing including extreme morphologies resembling the species *subeumela*, *cyclodorsata* and *hoelderi*. He believed that it proved the phylogenetic connection between *S. galar* and that group of species. Unfortunately, the specimens studied by Zeiss are crushed, but analysis of casts of the holotype and one of the two paratypes confirms that a smaller whorl-thickness compared with *S. galar* must be added to the differences correctly stated by Zeiss. With this qualification, the specimens studied from southern Spain fit well within the morphological spectrum of *S. galar thieli* (Text-fig. 5). Compared with the known specimens from southern Germany, populations from southern Spain include smaller forms and generally show more evolute shells, with comparable rib densities only for primaries; secondaries are less numerous. Size and whorl thickness separate this species from *S. galar* and *S. nusplingensis*. The younger *S. cyclodorsata* has a comparatively globose shell. Other Oxfordian–Kimmeridgian *Sutneria* have coarser and/or more distinct sculpture.



TEXT-FIG. 6. A–E, *Sutneria galar* (Oppel, 1863); microconchs; Planula Zone (Galar Subzone). A, FA-4.219; Fuente Alamo; Bed 4. B, FA-4.200; Fuente Alamo; Bed 4. C, FA-4.207; Fuente Alamo; Bed 4. D–E, PL-HG.C.101; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones. F–T, *Sutneria galar thieli* Zeiss (1979); microconchs. F, Slg.Erl.M1; holotype (cast); Drügendorf/Ofr; Platynota Zone. G, Slg.Erl.M3; paratype (cast); Ebermannstadt/Ofr; Platynota Zone. H, FA-10.71; Fuente Alamo; Bed 10, Platynota Zone. I–J, SPN_1-27.184; Navalperal; Bed 27; Planula Zone (Galar Subzone). K, $Z.G_2$.5b; Sierra Gorda-Alcaudique; upper part of Bed 5; Planula Zone (Galar Subzone). L–M, SPN_1-24.120; Navalperal; Bed 24; Planula Zone (Galar Subzone). N, NV-21A.19; Navalperal; Bed 21A; Platynota Zone. O, FA-506.50; Fuenta Alamo; Bed 506; Platynota Zone. P, SPN_1-27.185; Navalperal; Bed 27; Planula Zone (Galar Subzone). Q–R, PL-HG.A.1; Puerto Lorente; ferruginized surface beneath alternating marls, marly limestones and limestones; Planula Zone (Galar Subzone). S, FA-6.94; Fuenta Alamo; Bed 6; Platynota Zone. T, PL-8t.53; Puerto Lorente; upper part of Bed 8; Platynota Zone. U, *Sutneria nusplingensis* Fischer (1913); FA-6.35; microconch; Fuente Alamo; Bed 6; Platynota Zone. V–W, *Sutneria praecursor*; original (cast) figured by Dieterich (1940, pl. 2, fig. 1); microconch; Nusplingen/Würtemberg; 'Weisser Jura β'. Bed numbers follow Olóriz (1978) and Rodríguez-Tovar (1993). All $\times 1{\cdot}5$.

Occurrence. According to present data, this species ranges from the uppermost Oxfordian (upper Planula Zone) to the lowermost Kimmeridgian (Platynota Zone) in southern Spain. In southern Germany, it has been recorded only in the Platynota Zone.

REMARKS ON THE SIGNIFICANCE OF THE AMMONITES STUDIED

Previous studies considered *Sutneria* to be a typical component of ammonite assemblages of epicontinental seas surrounding the Tethys (Ziegler 1958). This is especially true during the latest Oxfordian and Early Kimmeridgian. Rare incursions into the Subboreal realm were first interpreted as facies-controlled and related to limestone intercalations (Callomon *et al.* 1971), but later research proved otherwise (Birkelund *et al.* 1983). Recent research has provided similar evidence from other siliciclastic basins, such as northern central Mexico (Olóriz, unpublished) and the Lusitanian Basin in western Portugal (Atrops and Marques 1986). It seems, therefore, that other factors, less directly related to depositional conditions, determined the geographical distribution of this genus.

The increasing rarity of southern records of *Sutneria* has been widely acknowledged and, when records are compared, there are stratigraphical differences between the acme of *Sutneria platynota* in southern Germany and that in south-eastern France (Ziegler 1981). Ecostratigraphical processes, at present poorly understood, could be envisaged to explain this, but the relative impoverishment in the southern records of *Sutneria* could be related also to other geological factors affecting Tethyan and southern peri-Tethyan areas, at least during the latest Oxfordian and the earliest Kimmeridgian.

Comparison of *Sutneria* records in epicontinental (Prebetic) *vs* epioceanic (Subbetic) deposits in southern Spain shows a marked difference. Both *S. galar* and *S. platynota* are more common in epicontinental deposits, but stratigraphical condensation and preservation in the Subbetic *ammonitico rosso* facies could seriously affect comparative analyses. These epicontinental successions of alternating limestones and marls can be over three hundred to four hundred times thicker than the bio-chronostratigraphical equivalent in the nodular limestones, such as Subbetic *ammonitico rosso* and related facies, deposited on distal pelagic swells.

Analysis of the epicontinental deposits enables the recognition of a tectonic pulse with erosional events on the South Iberian margin around the Oxfordian-Kimmeridgian boundary (Rodríguez-Tovar 1993). Marques *et al.* (1991) called this the 'final Oxfordian crisis', to which the significant increase in subsidence in epicontinental areas during the early Kimmeridgian can be related, as can reworking phenomena affecting the uppermost Oxfordian and lowermost Kimmeridgian in distal epioceanic areas with condensed sedimentation. In this context, it is significant that the relative biostratigraphical ranges of *S. galar* and *S. platynota* in the Prebetic and Subbetic remain unaffected except in extremely condensed and/or reworked deposits. This suggests that not only ecological factors determined the record of these species in these southern areas, as traditionally interpreted, but that other geological factors could have had a considerable influence.

In the Tethys, east of southern Spain, stratigraphical condensation and the discontinuous ammonite record must be largely responsible for the 'extreme scarcity of *Sutneria platynota* in northern Italy' described by Sarti (1988). This was confirmed by Cecca and Santantonio (1988) in the central Apennines, and previously by Wendt (1971) in Sicily. The record of rare *S. platynota* from a neptunian dyke in the western Lessinian Alps near Sant'Anna d'Alfaedo (Benetti *et al.* 1990) is consistent with our ideas. A similar context can be inferred for Romania (see Barbulescu 1969; Avram 1988), where the uppermost Oxfordian is recognized only locally in nodular limestones with *S. galar* (Preda 1973 *in* Avram 1988). In North Anatolia, *S. platynota* (Reinecke) has also been found in condensed deposits (Cope 1991).

As we commented above, records of *Sutneria* from around the Oxfordian-Kimmeridgian boundary in North Africa are also scarce. Sedimentation was clearly affected by important increases in siliciclastics and even emersions at that time, and discontinuity in the ammonite record is well known (Atrops and Benest 1992). In this case, it is significant that in the younger horizons containing *S. platynota*, the species is represented by the younger morphotype C of Schairer (1970) (cf. Atrops and Benest 1982).

Increased siliciclastics, sampling difficulties and probable stratigraphical discontinuities prevent precise control of the *Sutneria* record around the Oxfordian-Kimmeridgian boundary in the classic Montejunto region (western Portugal), as deduced by Atrops and Marques (1986). This is also the case in the Iberian Chain, as can be seen in the overview by Meléndez *et al.* (1990).

In this context, the record of 144 *Sutneria* specimens collected bed-by-bed around the Oxfordian-Kimmeridgian boundary on the South Iberian margin represents a valuable source of information on the best known southern assemblage of this genus. Data obtained for the upper Planula Zone (uppermost Oxfordian) and the Platynota Zone (lowermost Kimmeridgian) enables us to: (1), form a more exact idea of the distribution of *Sutneria* in southern areas related to the Tethys during this interval; (2), undertake an initial evaluation of the differences between these southern populations and the previously better known populations from southern Germany and northern Switzerland; and (3), recognize the role of the geological factors that prevented the straightforward, traditional interpretation of the *Sutneria* record, particularly in epioceanic areas, on the basis of strictly palaeobiological and palaeoecological considerations.

From a biostratigraphical viewpoint, the following appear to be well established and/or significant facts: (1), strongly sculptured specimens of *Sutneria platynota* ('Formengruppe' A of Schairer (1970)) are restricted to the basal part of the Kimmeridgian, even in condensed limestones; (2), other morphotypes of *S. platynota* ('Formengruppe' B and C of Schairer (1970)) have a wider distribution, generally including the complete stratigraphical range of this species in the study area; (3), the rare *S. nusplingensis* is found at the very base of the Platynota Zone; (4), *S. galar thieli* ranges from the upper Planula Zone to the Platynota Zone; and (5), there is no bed with identified ammonites between the last recorded occurrence of *S. galar* and the first appearance of *S. platynota*.

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