

AALENIAN *TMETOCERAS* (AMMONOIDEA) FROM IBERIA

Taxonomy, Habitats, and Evolution

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Abstract

Several hundred Aalenian *Tmetoceras* from the Iberian Peninsula (N Lusitanian Basin, Asturias, Basque-Cantabrian Basin, NE Cameros, NW Iberian Basin, Aragonese Platform, Tortosa Platform, Castilian Platform, Majorca and Betic Basin) have been reviewed. Two species of Aalenian *Tmetoceras* have been identified on the basis of morphological, biochronological and palaeobiogeographical data: *T. scissum* and *T. regleyi*.

T. scissum was dominant among the *Tmetoceras* populations developed in the Betic and Lusitanian basins during Opalinum, Murchisonae and Bradfordensis biochrons. Populations composed by evolute individuals of *T. scissum* inhabited shelfal or oceanic environments. A chronocline, from rectiradiate and primitive forms to flexicostate and derived forms, can be recognized in these populations of *T. scissum*. In contrast, shallow epicontinental platforms were inhabited by involute individuals of *T. regleyi*. This second species was phylogenetically derived from *T. scissum*, representing an adaptive radiation from populations of shelfal or oceanic basins to populations of epicontinental platforms.

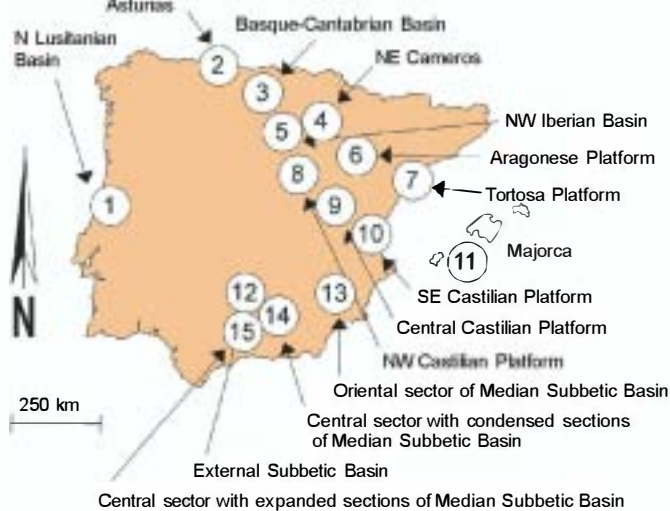


Figure 1. Geographic location of Aalenian areas distinguished in the Iberian Peninsula.

1. INTRODUCTION

Tmetoceras, having a worldwide geographic distribution, is quite common in the Iberian Peninsula, where it occurs from Aalensis to Bradfordensis biozones. More than 600 specimens of Aalenian *Tmetoceras* have been studied in this work. They come from 15 different areas (Figure 1), where a detailed biostratigraphic and biochronological framework has been recently established in several works (cf. Fernández-López *et al.* 1997). The main purpose of the present work is to provide a taxonomic distinction of the Aalenian *Tmetoceras* recorded in the Iberian Peninsula interpreting the evolutionary processes that occurred in this taxonomic group.

2. TAXONOMY

The present taxonomic analysis of Aalenian *Tmetoceras* from the Iberian Peninsula is based on 611 specimens. Morphological analysis of the shells have been performed evaluating the geometrical shape of the shells (including dimensional parameters, D= shell diameter, U= umbilical diameter, Ne/2= number of ribs per half whorl), and the features of the suture lines.

The subfamily Tmetoceratinae was established by Spath (1936) as belonging to the Hildoceratidae, but he gave no diagnostic characters for classification. This systematic attribution has been accepted by many authors: Arkell (1957), Donovan (1958), Westermann (1964), Geczy (1967), Westermann and Riccardi (1972), Donovan *et al.* (1981), Hillebrandt and Westermann (1985), Ureta (1985), Poulton and Tipper (1991), Henriques (1992), Rulleau (1995). However, some authors have proposed different systematic positions for this taxonomic group. Maubeuge (1955) changed the group to the category of family, including it in the Harpocerataceae. Dubar and Mouterde (1961) did not accept the subfamily Tmetoceratinae, and they considered *Tmetoceras* to be a genus of the subfamily Grammocerotinae. Later, Tintant and Mouterde (1981) considered the family Tmetoceratidae as belonging to the Hammatocerataceae.

The subfamily Tmetoceratinae contains one single genus: *Tmetoceras*. From a phylogenetic point of view, *Tmetoceras* is considered narrowly related to the Grammocerotinae (Arkell, 1957; Geczy, 1967; Donovan *et al.* 1981). *Tmetoceras* would have derived from a Mediterranean species of *Dumortieria* or *Catulloceras* during the late Toarcian. This interpretation is based on the morphological similarity of the shells of these two taxonomic groups. The appearance of the first representatives of *Tmetoceras* implied the loss of the keel and the acquisition of a ventral groove. Schindewolf (1964) argued that septal sutures of *Dumortieria* are dissimilar to those of *Tmetoceras*, the latter displaying a bifid, narrow, internal lobe, instead of a trifid one. Furthermore, some morphological characters of *Tmetoceras* are rare in Hildoceratids: straight ribbing, median ventral groove and deep constrictions. However, according to Schindewolf, the disparity in septal sutures does not justify a direct origin of *Tmetoceras* from *Lytoceras* or *Alocolytoceras*, as suggested by Salfeld (1920, 1924) and Heidorns (1936). On the basis of these morphological differences, Schindewolf (*op. cit.*) proposed classifying this strongly isolated genus as the family Tmetoceratidae belonging to the Hammatocerataceae.

2.1. Genus *Tmetoceras* Buckman, 1892

Type-species: "*Ammonites scissus*" Benecke (1865, p. 170, pl. VI, fig. 4).

Diagnosis: Shells of medium size (Dmax. = 20-80 mm). Planulate coiling, subcircular to subrectangular whorl section. The ribbing is simple, sharp, wiry and interrupted on the venter by a median groove.

Discussion: *Tmetoceras* was proposed by Buckman (1892), referring to the type-species "*Ammonites scissus*" of Benecke (1865). This species was formerly attributed to quite different genera by distinct authors: *Simoceras* (Meneghini, 1867; Vacek, 1886), *Cosmoceras* (Gottsche, 1878; Buckman, 1883), *Parkinsonia* (Zittel, 1881; Gregorio, 1886a, b, c; Gemmellaro, 1886; Prinz, 1904), *Dumortieria* (Haug, 1892) and *Catulloceras* (Lanquine, 1929).

Buckman (1892) proposed including the genus *Tmetoceras* in the family *Polymorphidae*. However, most recent authors include it in *Hildoceratidae*, as the subfamily *Tmetoceratinae*.

Several nominal species of *Tmetoceras* have been proposed: "*Ammonites scissus*" Benecke (1865); "*Ammonites Regleyi*" Thiollière in Dumortier (1874); "*Cosmoceras Hollandae*" Buckman (1883); "*Parkinsonia difalensis*" Gemmellaro in Bonarelli (1893); "*Tmetoceras circulare*" Buckman (1905); "*Tmetoceras recticostatum*" Sato (1954); "*Tmetoceras dhanarajatai*" Sato (in Komalarjum and Sato, 1964); "*Tmetoceras kirki*" Westermann (1964) and "*Tmetoceras tenue*" Westermann (1964).

Sexual dimorphs of *Tmetoceras* were originally recognized among the Alaskan populations (Westermann, 1964). This author illustrated macroconchs with simple aperture, which are preceded by a wide constriction, and small microconchs bearing short lateral lappets. The maturity of the specimens is evidenced by the uncoiling of the umbilical seam. The ribbing persists isocostate and strong up to the end of the ontogenic development. Microconchs were nominally distinguished as representatives of the subgenus *Tmetoites* (Westermann, 1964).

Distribution: *Tmetoceras* is a pandemic genus widely distributed in the Tethyan Realm. It is scarcely registered apart from certain specimens in southern areas of the Boreal Realm. However, these rare specimens of the Boreal Realm probably do not represent demic individuals, and they can represent drifted shells. First representatives of the genus occur in the Aalensis Biochron of Mediterranean (or West Tethyan) regions. The last representatives have been referred to the late Aalenian or the Early Bajocian in East-Pacific Subrealm.

In the Iberian Peninsula, specimens of *Tmetoceras* range from uppermost Toarcian (Aalensis Biozone) to the upper Aalenian (Bradfordensis Biozone) with maximum frequency in Opalinum and Bradfordensis biozones. Specimens belonging to post-Bradfordensis deposits have been identified as reelaborate elements. Consequently, these specimens are older than the encasing rock (Fernández-López *et al.*, 1997).

Aalenian specimens of *Tmetoceras* from the Iberian Peninsula studied in the present work correspond to two species: *T. scissum* and *T. regleyi*.

2.1.1. *Tmetoceras scissum* (Benecke, 1865).

Figures 2, 3, 8A-N, 9F-Q

- 1865 *Ammonites Scissus* Benecke, p. 170, pl. 6., fig. 4.
1878 ? *Cosmoceras Regleyi* Thiollière: Gottsche, p. 16, pl. 2, fig. 3
1886 *Simoceras scissum* Benecke: Vacek, p. 103, pl. 16, figs. 15-17.
1886a *Parkinsonia Regleyi* Thiollière: Gregorio, p. 673, pl. 2, fig. 9.
1886b *Parkinsonia scissus* Benecke (= *Regleyi* Thiol.): Gregorio, pl. 24, figs. 19, 21-24, 26.
1886b *Parkinsonia scissus* Benecke var. *ghesus* De Greg.: Gregorio, pl. 24, fig. 25.
1886c *Parkinsonia scissus* Benecke: Gregorio, p. 17, pl. 10, figs. 19, 21-24, 26.
1886c *Parkinsonia scissus* Benecke Mut. *ghesus*: Gregorio, p. 17, pl. 10, fig. 25.
1892 *Tmetoceras scissum* Benecke: Buckman, p. 273, pl. 48, figs. 1-7.
1900 *Tmetoceras scissum* Benecke: Burckhardt, p. 31, pl. 22, figs. 1,2.
1903 *Tmetoceras* aff. *Gemmellaroi* Fucini: Burckhardt, p. 21, pl. 2, figs. 4,5.
1904 *Parkinsonia (Tmetoceras) scissa* Benecke: Prinz, p. 130, pl. 16, fig. 2, pl. 20, fig. 3.
1905 *Tmetoceras circulare* Buckman: Buckman, p. 170.
1907 *Tmetoceras circulare* Buckman: Buckman, pl. 48, figs. 1-3.
1923 *Tmetoceras scissum* Benecke: Roman and Boyer, p. 36, pl. 6, fig. 8.
1933 *Tmetoceras scissum* (Benecke): Arkell, pl. 33, fig. 4.
1939 *Tmetoceras scissum* (Benecke): Ramaccioni, p. 181, pl. 12, fig. 7.
1951 *Tmetoceras regleyi* (Thiollière) Dumortier: Frebold, p. 18, pl. 15, figs. 1-4.
1954 *Tmetoceras recticostatum* sp. nov.: Sato, p. 118, pl. 13, figs. 1-18.
1955 *Tmetoceras scissum* (Benecke): Maubeuge, p. 17, pl. 2, fig. 1.
1955 ?*Tmetoceras* sp.: Imlay, p. 89, pl. 12, figs. 7-12.
1964 *Tmetoceras scissum* (Benecke): Westermann, p. 428, pl. 72, figs. 1,2.
1964 *Tmetoceras regleyi* (Dumortier): Komalarjum and Sato, p. 157, pl. 6, figs. 10-12, 14, 15.
1967 *Tmetoceras scissum* (Benecke): Geczy, p. 160, pl. 35, figs. 3-7, pl. 64, figs. 73-74.
1967 *Tmetoceras scissum* (Benecke): Seyed-Emami, p. 46, pl. 1, fig. 26.
1969 *Tmetoceras* cf. *Tmetoceras scissum* (Benecke): Frebold *et al.* p. 21, pl. 1, figs. 1-5.
1970 *Tmetoceras* aff. *scissum* (Benecke): Fischer, p. 601, pl. 4, fig. 5.
? 1971 *Tmetoceras scissum* (Benecke): Patruilus and Popa, p. 136, pl. 3, fig. 2.
1972 *Tmetoceras scissum* (Benecke, 1865): Westermann and Riccardi, p. 22, pl. 1, figs. 1-5.
1972 *Tmetoceras* cf. *flexicostatum* Westermann, 1964: Westermann and Riccardi, p. 23, pl. 1, fig. 6.
1973 *Tmetoceras scissum* (Benecke): Imlay, p. 59, pl. 2, figs. 1-6.

- 1974 *Tmetoceras scissum* (Benecke): Suárez-Vega, p. 167, pl. 14, fig. 3.
 1985 *Tmetoceras* gr. *scissum* (Benecke): Venturi, p. 85, fig. 133.
 1985 *Tmetoceras scissum* (Benecke): Bogdanic *et al.*, pl. 1, fig. 1.
 1985 *Tmetoceras scissum* (Benecke): Ureta, p. 180, pl. 5, figs. 1, 3.
 1988 *Tmetoceras scissum* (Benecke): Linares *et al.*, pl. 1, fig. 5.
 1990 *Tmetoceras scissum* (Benecke): Callomon and Chandler, pl. 1, fig. 1a, b.
 1991 *Tmetoceras scissum* (Benecke, 1865): Poulton and Tipper, pl. 1, figs. 1-32.
 1991 *Tmetoceras scissum* (Benecke): Hernández-Molina *et al.*, p. 96, fig. 13, 1.
 1992 *Tmetoceras* cf. *scissum* (Benecke, 1865): Henriques, p. 28, pl. 2, fig. 11.
 1992 *Tmetoceras scissum* (Ben.): Westermann, pl. 23, fig. 3., pl. 52, fig. 6.
 1994 *Tmetoceras scissum* (Benecke, 1865): Callomon and Chandler, p. 27, pl. 5, fig. 3, pl. 8, figs. 2, 3, 4.
 1994 *Tmetoceras scissum* (Benecke): Elmi and Rulleau, p. 154, pl. 2, figs. 5-6.
 1995 *Tmetoceras circulare* Buckman: Rulleau, pl. 19, fig. 5.

Material: 558 Aalenian specimens of the Iberian Peninsula have been studied. 337 Opalinum specimens of *T. scissum* have been obtained from Lusitanian Basin (34), Iberian Basin (110) and Betic Basin (193). 88 Murchisonae specimens have been obtained from the Betic Basin. 129 Bradfordensis specimens of this species have been obtained from Lusitanian Basin (30), Iberian Basin (27) and Betic Basin (72). 4 specimens included in Concavum deposits of the Iberian Basin have been taphonomically determined as reelaborate elements.

Diagnosis: Evolute macro- and microconchs (U/D= 40-60 % in post-juvenile stages). The ribbing is thin, acute, prominent and distant. The septal suture is moderately complex. The lateral lobe is tight and deeper than the siphonal lobe (Figure 2).

Description: Adult shells are of medium size, from microconchs reaching 20 mm of maximal diameter to macroconchs exceeding 80 mm in diameter. They have evolute coiling, increasing the values of umbilical ratio in the successive stages of the ontogenic development, and attaining the highest on the adult body chamber (Figure 3). The umbilical wall is moderately steep. Whorls vary in section from subquadrate to subcircular contour, and they have slightly convex flanks.

The ornamentation consists of simple ribs, varying in densities between 10 and 30 per half whorl (20 on the average; Figure 3). Ribs are thin, acute, prominent and distant. The width of the ribs is narrower than the intercosta spaces. For equivalent diameters, microconchs show sparse ribbing and they are more evolute than the macroconchs. The ribbing is interrupted in the ventral region by a deep and straight median groove. Early Opalinum representatives exhibiting three to five constrictions per whorl are common in Betic areas, as noted in some Italian specimens (cf. Benecke, 1865, pl. 6, fig. 4; Vacek, 1886, pl. 16, figs. 15-17; Ramaccioni, 1939, pl. 12, fig. 7).

Primitive Aalenian representatives of *T. scissum* have acute and rectiradial ribbing. Phyletically derived forms of the Bradfordensis Biochron show a blunt and flexicostate pattern, and higher density of ribbing, over ontogenetic development. Transient forms in

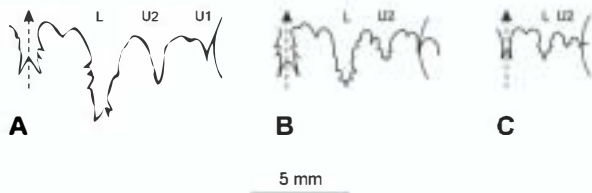


Figure 2. Septal suture of *T. scissum*. (A and B) Specimen SG107.1; Opalinum Biozone; S. Guião, Degracias (N Lusitanian Basin). (C) Specimen SM20/15; Opalinum Biozone; Santa Mera (Asturias).

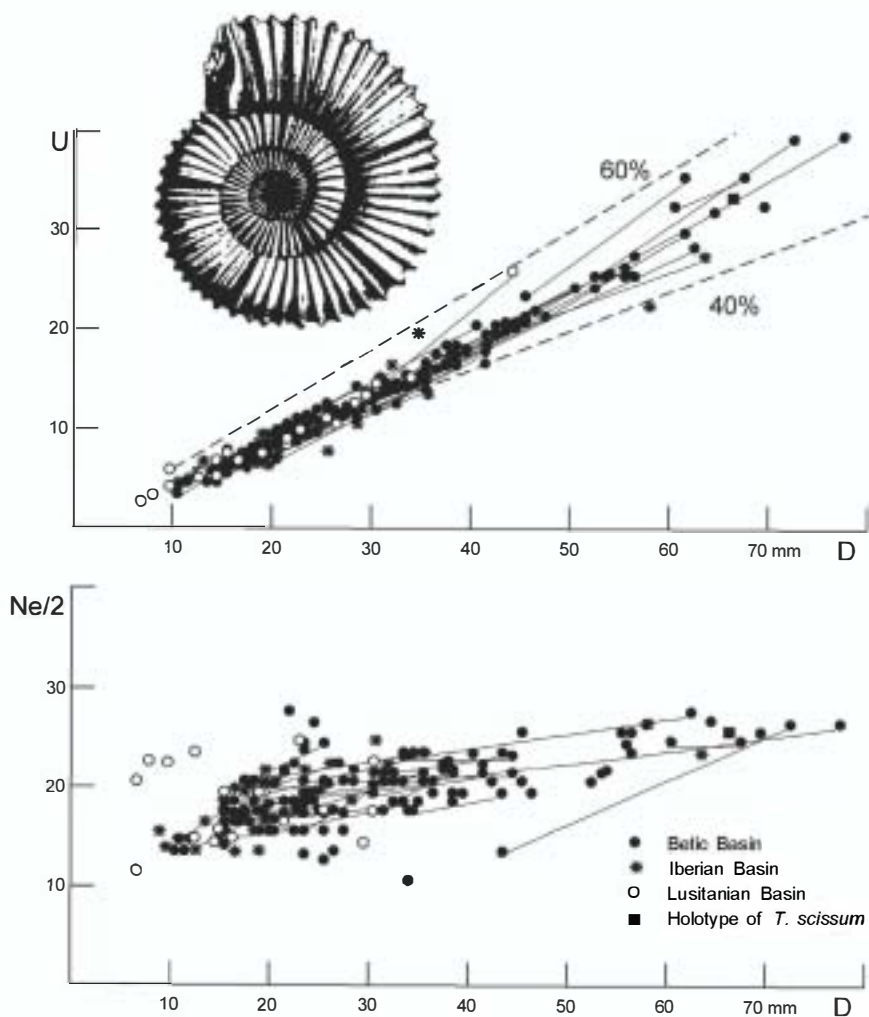


Figure 3. Values of umbilical diameter and number of ribs per half-whorl of *T. scissum*.

the Murchisonae Biochron have flexicostate ribs in inner and intermediate whorls, whilst they display reticostate ribs in external whorls. Consequently, a chronocline may be identified among the Aalenian populations of *T. scissum*, from the Opalinum, primitive representatives to the phyletically derived forms of the Bradfordensis Biochron (Figure 4). This chronocline can be interpreted as a paedomorphic result of a proterogenetic evolutionary process, associated with a delay of the somatic development in the younger representatives (cf. Dommerguès *et al.*, 1986, 1989; McNamara, 1990). In this way, phyletically derived representatives of the Bradfordensis Biochron can be considered neotenic forms making up a paedomorphocline.

Discussion and affinities: Very evolute and sparsely ribbed forms showing subcircular whorls, as in the holotype of *T. circulare* Buckman (1905; 1907, pl. 48, figs. 1-3; cf. Rulleau, 1995, pl. 19, fig. 5), are very common in the Betic Basin. They represent a primitive morphotype of *T. scissum*.

According to Westermann (1964, p. 435), *T. reticostatum* Sato (1954, p. 118, pl. 13, figs. 1-18) likewise represents a synonym of *T. scissum*. The syntypes of this species dis-

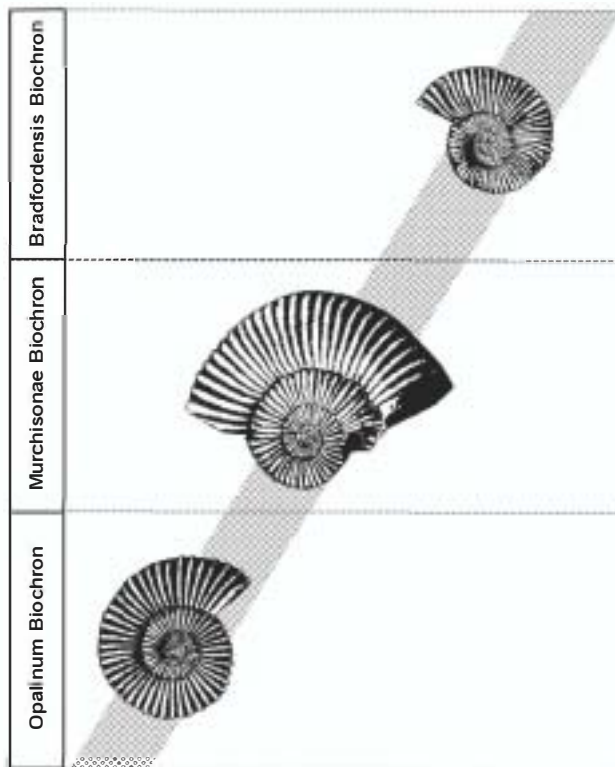


Figure 4. Pedomorphocline of *T. scissum* in shelfal basins during Opalinum, Murchisonae, and Bradfordensis biochrones.

play many similarities in the ornamentation with the transients or the phyletically derived forms of *T. scissum* found in the Betic Basin.

T. kirki, including the two subspecies *T. kirki kirki* and *T. kirki flexicostatum* (Westermann, 1964, p. 437, pl. 72, figs. 4-10), is abundant in upper Aalenian deposits of the East Pacific (Canada and Alaska). It is morphologically close to the more evolved forms of *T. scissum*. However, according to the original diagnosis, *T. kirki* has an externally narrowly interrupted and sometimes subcontinuous ribbing. On the other hand, *T. kirki* is a species provincially restricted to the East Pacific Subrealm.

T. dhanarajatai Sato (1964 in Komalarjum and Sato, 1964, p. 155, pl. 6, figs. 1-9, 16-18; holotype redrawn in Westermann, 1992, pl. 14, fig. 9), a species from Thailand, is more evolute than *T. scissum*, showing lower values of rate of whorl expansion and denser ribbing. This species from Thailand is so distinct that it is hard to confuse with any other species of *Tmetoceras*.

Distribution: *T. scissum* occurs in the Aalenian of Lusitanian, Basque-Cantabrian, Iberian and Betic basins, and Majorca island, being abundant from Opalinum to Bradfordensis biochrones in the Lusitanian and Betic basins. *T. scissum* has been commonly recorded in lower and middle Aalenian deposits (Opalinum, Murchisonae and Bradfordensis biozones) in the northern margins of the West Tethyan Subrealm, from North Africa and western Europe eastward to southeast Asia and beyond, and around the Pacific Ocean, in-

cluding the East-Pacific Subrealm. The species seemingly attain a pandemic distribution (Fernández-López *et al.*, 1997). In the Mediterranean and Submediterranean provinces it has also been recorded in deposits of the upper Toarcian (Aalensis Biozone). However, no late Aalenian (Concavum Biochron) specimens of this species have been found in the Iberia Peninsula. The presumed Concavum specimen of England determined as *T. scissum* by Callomon and Chandler (1994, pl. 6, fig. 3) may belong to the genus *Fontannesia*.

2.1.2. *Tmetoceras regleyi* (Dumortier, 1874).

Figures 5, 6, 9A-E

- 1874 *Ammonites regleyi*: Dumortier, p. 119, pl. 31, figs. 8–9 (holotype).
 1883 *Cosmoceras Hollandae*, var.: Buckman, pl. 1, fig. 2.
 1886 *Parkinsonia difalensis*: Gemmellaro, p. 10.
 1892 *Tmetoceras Hollandae*, S. Buckman: Buckman, p. 275, pl. 48, figs. 11-12.
 1892 *Tmetoceras scissum* (Benecke) var.: Buckman, pl. 48, figs. 8-10.
 1893 *Tmetoceras difalense* Gemm. n. sp.: Bonarelli, p.237.
 1905 *Tmetoceras Regleyi* (Thiollière): Buckman, p. 170.
 1923 *Tmetoceras scissum* (Benecke): Roman and Boyer, p. 36, pl. 6, figs. 6 (holotype), 7-8.
 ? 1963 *Tmetoceras scissum* (Benecke): Rieber, p. 9, pl. 8, figs. 2, 3.
 ? 1977 *Tmetoceras scissum* (Benecke): Dietl, pl. 1, fig. 3.
 1985 *Tmetoceras scissum* (Benecke, 1865): Schlegelmilch, pl. 3, fig. 5 (holotype).
 1985 *Tmetoceras scissum* (Benecke): Ureta, p. 180, pl. 5, fig. 2.
 1994 *Tmetoceras scissum* (Benecke, 1865): Callomon and Chandler, p. 27, pl. 5, fig. 2.
 1994 *Tmetoceras scissum* (Benecke): Elmi and Rulleau, p. 154, pl. 2, figs. 5- 6.
 1995 *Tmetoceras scissum* (Benecke): Rulleau, pl. 19, figs. 6-7, 9–12.
 1995 *Tmetoceras scissum* (Benecke) morphotype *hollandae* Buckman: Rulleau, pl. 19, fig. 8.

Material: 53 specimens from the Iberian Peninsula have been studied. They are mainly of the Tortosa Platform (34), the NW Iberian Basin (6) and the Basque-Cantabrian Basin (4). In the Betic Basin only a few specimens have been found.

Diagnosis: Involute macro- and microconchs (U/D= 30-50% in post-juvenile stages). Sections are subcircular with markedly convex flanks. Dense ribbing with wide and blunt ribs presenting a sinuous pattern. The septal suture is simple and scarcely cut, with lateral and siphonal lobes attaining approximately the same depth (Figure 5).

Description: Shells of medium size, including macroconchs and microconchs. Moderately involute coiling, with values of umbilical ratio ranging from 0.30 to 0.50 (Figure 6). Umbilical wall is markedly steep providing a deep umbilical region. Whorl section is subcircular with convex strongly flanks. The venter is interrupted by a discrete median groove, which represents the external interruption of the ribs.

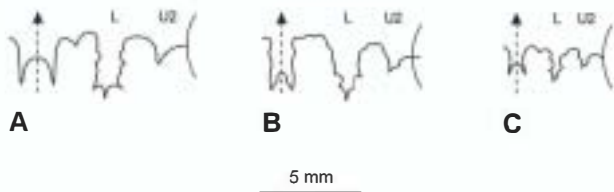


Figure 5. Septal suture of *T. regleyi*. (A) Specimen 5SS126/14; Bradfordensis Biozone; Coll de Soms (Tortosa Platform). (B) Specimen CN24/1; Opalinum Biozone; Canales de la Sierra (NW Iberian Basin). (C) Specimen CN24/9; Opalinum Biozone; Canales de la Sierra (NW Iberian Basin).

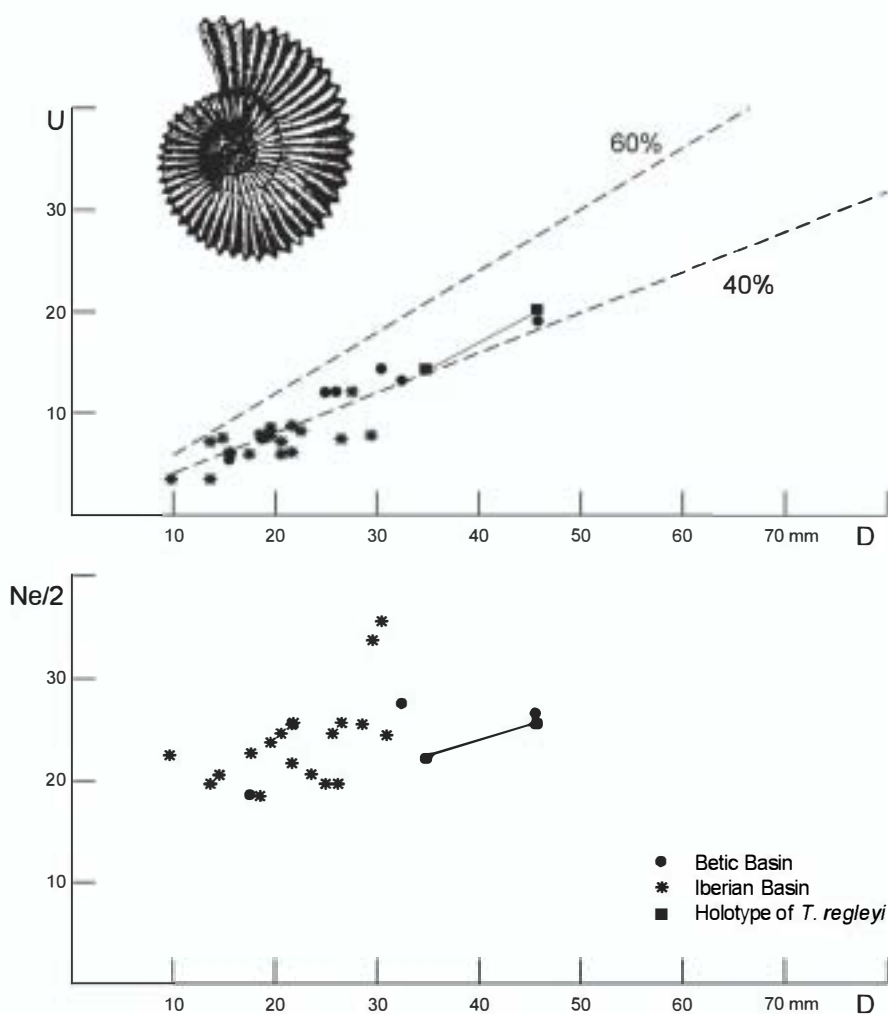


Figure 6. Values of umbilical diameter and number of ribs per half-whorl of *T. regleyi*.

The ornamentation consists of simple ribs, with densities varying of 20 to 35 per half whorl (Figure 6). Ribs are wide and blunt, their width being greater than intercosta spaces.

The microconchs of *T. regleyi* have not yet been described. The specimen shown in Figure 9C is a microconch. The maturity of the small microconchs bearing short lateral lappets is indicated by the uncoiling of the umbilical seam.

Discussion and affinities: The name *regleyi* was introduced by Dumortier (1874, p. 119) for a species that included in its type-series a specimen previously determined as "*Ammonites Regleyi*" by Thiollière (in 1854 according to Dumortier).

Diverse *Tmetoceras* found in different European, epicontinental platforms show morphological characters of *T. regleyi* (see synonymy), although these distinctive morphotypes have been determined as *T. scissum* by different authors. The holotypes of *T. hollandae* (Buckman) and *T. difalense* (Gemmellaro) are also morphotypes of *T. regleyi*. However, certain coarser-ribbed specimens of *T. scissum* are morphologically close to *T. regleyi*, due to a pathological development (cf. "*Cosmoceras Hollandae*" in Buckman, 1883, pl. 1, fig. 2; "*Tmetoceras scissum*" in Buckman, 1892, pl. 48, figs. 4-7).

T. regleyi, phyletically derived from *T. scissum*, is close to the ancestral species of the genus. *T. scissum* and *T. regleyi* have very similar inner whorls. Nevertheless, some differences enable to distinguish these two species. *T. regleyi* is more involute, showing a greater rate of whorl expansion, and it bears blunt ribs wider than the intercosta spaces. Septal suture is also a distinctive character of these species: it is more simple in *T. regleyi* than in *T. scissum* (Figure 5). Constrictions in *T. regleyi* are not as prominent as in *T. scissum*.

Distribution: The oldest specimen exhibiting morphological characters of *T. regleyi* has been found in the upper part of the Opalinum Biochron (Comptum Subchron). Nevertheless, this species is commonly recorded in the Murchisonae and Bradfordensis biozones. The geographical range of *T. regleyi* is practically restricted to some European, epicontinental platforms (France, Italy, Great Britain, Germany). In the Iberian Peninsula, this species is common in shallow environments of outer platforms. In contrast, it is very scarce in shelfal or oceanic areas, as in the Lusitanian and Betic basins.

3. HABITATS, PALEOBIOGEOGRAPHY, AND EVOLUTION

Aalenian populations of *Tmetoceras* inhabited two separate habitats: epicontinental platforms and shelfal basins (Fernández-López *et al.*, 1997). Habitats of epicontinental platform were cratonic areas flooded by shallow marine waters. In contrast, habitats of shelfal basins were situated on the continental shelf showing open inarine and oceanic environments.

T. scissum (Benecke) was seemingly a pandemic species, inhabiting oceanic or shelfal environments in the Early Aalenian. However, some species of *Tmetoceras*, such as *T. regleyi* (Dumortier), *T. dhanarajatai* (Sato) and *T. kirki* Westermann were geographically restricted in very distant areas.

The first representatives of *T. scissum*, as the holotype, display a rectiradiate and acute ribbing during the Opalinum Biochron. Its populations inhabited oceanic or shelfal environments as in the Betic and Lusitanian basins. During the Murchisonae Biochron, the rectiradiate ribbing is replaced by flexicostate ribs in the inner whorls. During the Bradfordensis Biochron most of the representatives of this species show flexicostate ribbing through the successively stages of the ontogenetic development. This paedomorphocline can be tested by the successively recorded associations, from the Opalinum Biozone to the Bradfordensis Biozone, in the Betic Basin (Figure 7). Shelfal or oceanic, generalist forms of *T. scissum* disappeared in the Western Tethys or the Mediterranean Province in the latest Bradfordensis Biochron, but they survived in the East-Pacific Subrealm. In latest Bradfordensis Biochron or in earliest Concavum Biochron, *T. scissum* gave rise to *T. kirki*, a species restricted to the East-Pacific Subrealm (Westermann, 1964; 1992; Westermann and Riccardi, 1972; Bogdanic *et al.*, 1985; Hillebrandt and Westermann, 1985; Poulton and Tipper, 1991). Representatives of *T. kirki* marked the last stage in an evolutionary process that led from Mediterranean *Tmetoceras* of the Aalenis Biochron (late Toarcian) to East-Pacific *Tmetoceras* of the Concavum Biochron (late Aalenian). The first steps in this process led proterogenetically to the development of a blunt ribbing on the inner whorls, which persist on the adult body chamber of the latest representatives.

The coarser-ribbed and more robust forms of *Tmetoceras* found in the Western Tethys probably represent a provincially restricted species. *Tmetoceras scissum* and *T. regleyi* appeared to intergrade, but they were ecologically and biogeographically differentiated (Fernández-López *et al.*, 1997). Representatives of *T. regleyi* were distributed mainly in the Sub-Mediterranean and Northwest European provinces, inhabiting shallow

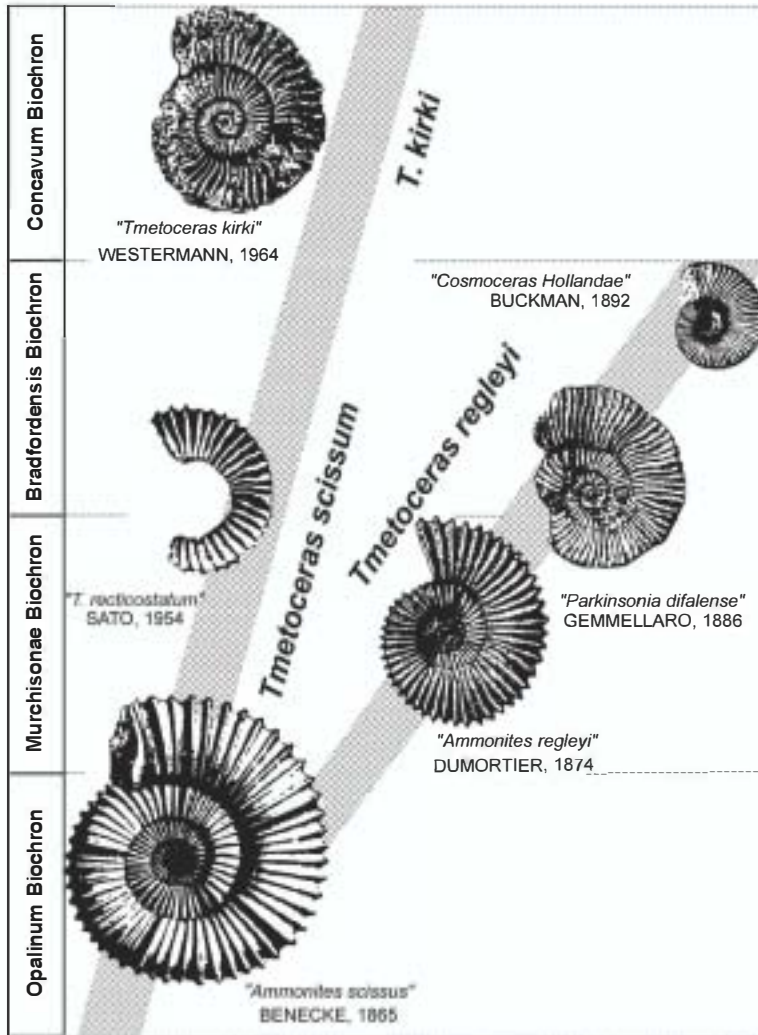


Figure 7. Phyletic relations among Aalenian species of *Tmetoceras*.

environments of epicontinental platforms. An adaptive radiation may have taken place in the Western Tethys during the Opalinum Biochrons (Comptum Subchron), giving rise to *T. regleyi* from *T. scissum*. Specialized forms of *Tmetoceras* (k-strategists such as the individuals of the species *T. regleyi*) are widespread in the epicontinental platforms around the Western Tethys during the Murchisonae and Bradfordensis biochrons. Epicontinental, specialized forms of *T. regleyi* became extinct in the latest Bradfordensis Biochron.

4. CONCLUSIONS

Aalenian specimens of *Tmetoceras* from the Iberian Peninsula correspond to two species: *T. scissum* and *T. regleyi*.

T. scissum was dominant among the *Tmetoceras* populations developed in the Betic and Lusitanian basins during Opalinum, Murchisonae and Bradfordensis biochrones. Populations composed by evolute individuals of *T. scissum* inhabited shelfal or oceanic environments. A chronocline, from rectiradiate and primitive forms to flexicostate and derived forms, can be recognized in these populations. This chronocline can be interpreted as a paedomorphic result of a proterogenetic evolutionary process, associated with a delay of the somatic development in the younger representatives. Phyletically derived representatives of the Bradfordensis Biochron can be considered to be neotenic forms comprising a paedomorphocline.

Shallow epicontinental platforms were inhabited by involute individuals of *T. regleyi*. This species was phyletically derived from *T. scissum*, representing an adaptive radiation from populations of shelfal or oceanic basins to populations of epicontinental platforms.

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Figure 8. Aalenian *Tmetoceras* of the Iberian Peninsula. (A) Immature macroconch of *Tmetoceras scissum*. CM78.40.8. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (B) Immature macroconch of *T. scissum*. CM78.40.5. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin), xl. (C) Immature macroconch of *T. scissum*. CMB.6.2. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (D) Immature macroconch of *T. scissum*. CMB.14.12. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (E) Immature macroconch of *T. scissum*. CMAL.(12-13). 1. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (F) Post-juvenile macroconch, incomplete phragmocone, of *T. scissum*. SG.107.1. Opalinum Biozone. S. Guíto, Degracias (N Lusitanian Basin). xl. (G) Post-juvenile individual, microconch?, of *T. scissum*. CM78.40.6. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin), xl. (H) Post-juvenile individual, microconch?, of *T. scissum*. CMAL.(12-13).3. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (I) Post-juvenile macroconch of *T. scissum*. M95-10. Comptum Subbiozone, Opalinum Biozone. Cabo Mondego (N Lusitanian Basin). xl. (J) Adult macroconch of *T. scissum*. CMB.23.2. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (K) Immature macroconch of *T. scissum*. CM78.40.9. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl. (L) Post-juvenile individual, microconch?, of *T. scissum*. JRi1.62.9. Comptum Subbiozone, Opalinum Biozone. Sierra de Ricote (Oriental sector of Median Subbetic Basin). xl. (M) Adult microconch of *T. scissum*. PV11/21. Comptum Subbiozone, Opalinum Biozone. Ribarroja (SE Castilian Platform). xl. (N) Post-juvenile individual, microconch?, of *T. scissum*. CMAL.(12-13).3. Comptum Subbiozone, Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). xl.

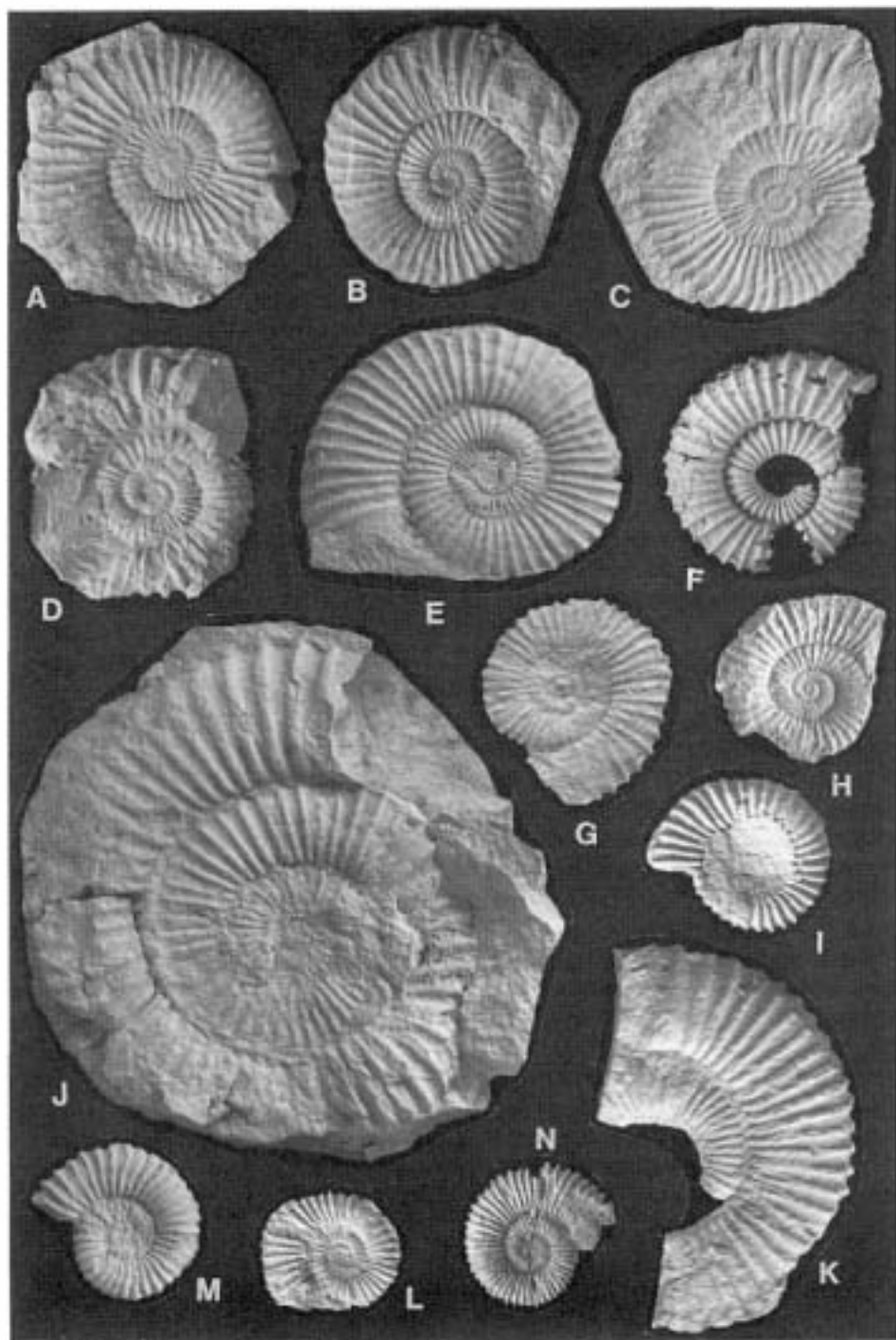
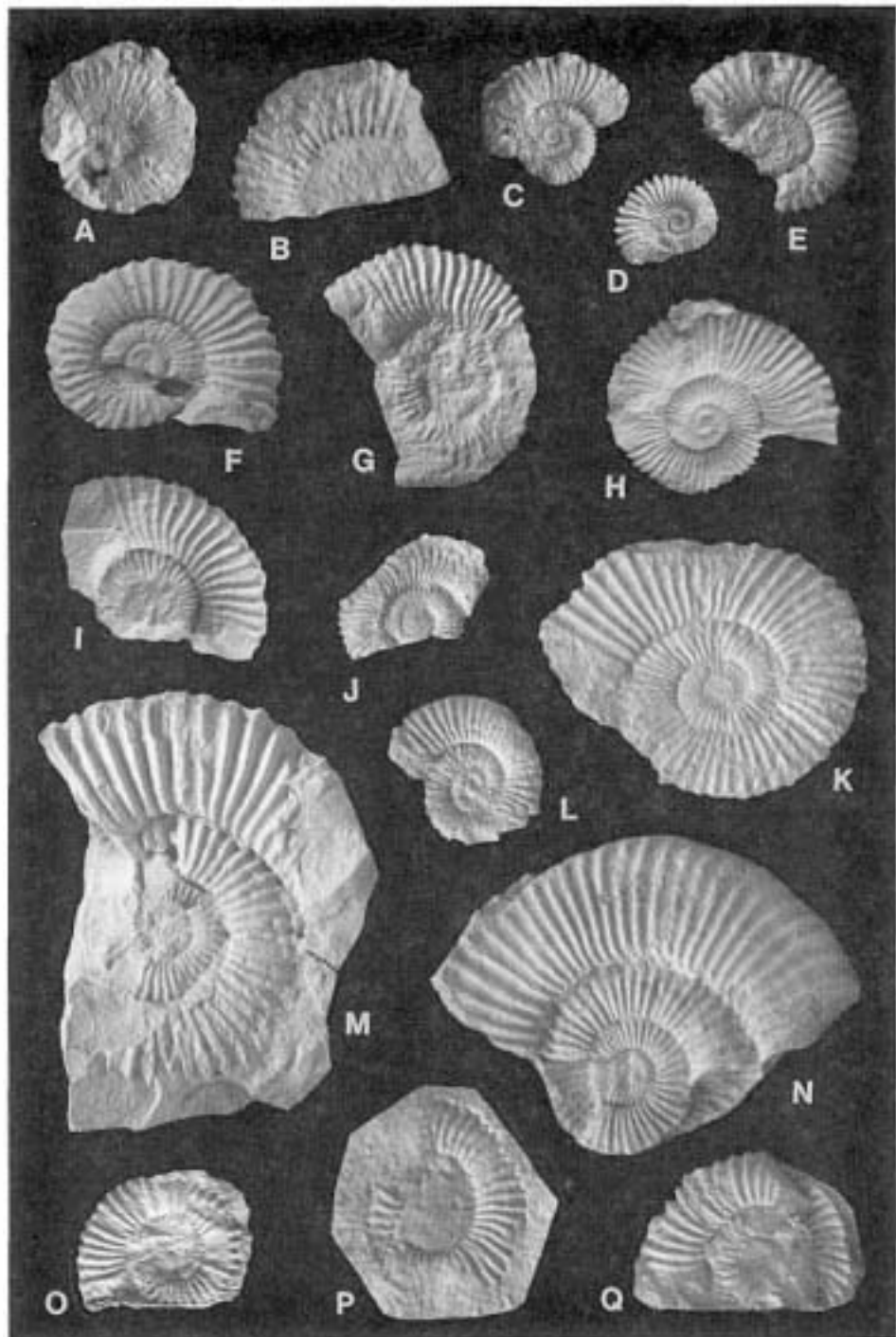


Figure 9. Aalenian *Tmetoceras* of the Iberian Peninsula. (A) Immature macroconch of *Tmetoceras regleyi*. SA447/1. Murchisonae Subbiozone, Murchisonae Biozone. San Andres (Basque-Cantabrian Basin). x1. (B) Immature macroconch of *T. regleyi*. 5SS126/23. Bradfordensis Biozone. Coll de Soms (Tortosa Platform). x1. (C) Adult microconch of *T. regleyi*. 5SS126/14. Bradfordensis Biozone. Coll de Soms (Tortosa Platform). x1. (D) Juvenile individual of *T. regleyi*. 5SS126/7. Bradfordensis Biozone. Coll de Soms (Tortosa Platform). x1. (E) Immature macroconch of *T. regleyi*. CN24/1. Comptum Subbiozone, Opalinum Biozone. Canales de la Sierra (NW Iberian Basin). x1. (F) Juvenile individual, microconch?, of *T. scissum*. MOA.16.22. Gigantea Subbiozone, Bradfordensis Biozone. Montillana (central sector with expanded sections of Median Subbetic Basin). x1. (G) Immature macroconch of *T. scissum*. CMAL.51.7. Gigantea Subbiozone, Bradfordensis Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (H) Immature macroconch of *T. scissum*. MOA.14.11. Gigantea Subbiozone, Bradfordensis Biozone. Montillana (central sector with expanded sections of Median Subbetic Basin). x1. (I) Immature macroconch of *T. scissum*. MOA.16.3. Gigantea Subbiozone, Bradfordensis Biozone. Montillana (central sector with expanded sections of Median Subbetic Basin). x1. (J) Post-juvenile individual of *T. scissum*. MOA.15.9. Gigantea Subbiozone, Bradfordensis Biozone. Montillana (central sector with expanded sections of Median Subbetic Basin). x1. (K) Immature macroconch of *T. scissum*. CMB.24.1. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (L) Adult microconch of *T. scissum*. CMB.21.15. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (M) Immature macroconch of *T. scissum*. CMB.22.1. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (N) Immature macroconch of *T. scissum*. CMB.24.2. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (O) Post-juvenile individual, microconch?, of *T. scissum*. CMB.22.12. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (P) Post-juvenile individual of *T. scissum*. CMB.21.13. Haugi Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1. (●) Adult microconch of *T. scissum*. CMB.26.1. Murchisonae Subbiozone, Murchisonae Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x1.



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