The mediterranean *Tropidoceras* (Ammonitina) in the Betic Cordilleras

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ABSTRACT

This reviews the mediterranean representatives of the genus *Tropidoceras* on the basis of the abundant material found in the Carixian in the Betic Cordilleras. All the exemplars studied are from the northern edge of the Subbetic Zone, although the genus is represented in other sequences in the basin.

The interest of this study lies in the fact that *Tropidoceras* were dominant in the mediterranean Middle Carixian and form the basis of the biostratigraphy. The abundance and diversity of the material enabled us to undertake a taxonomic study of the genus, allowing us to locate it between the closely related species of *Gemmellaroceras* and *Acanthopleuroceras*.

The existence of six morphospecies: *T. erythraeum*, *T. demonense* – *T. flandrini*, *T. calliplocum* – *T. mediterraneum* and *T. zitterli* (macro and microconch), in which it is possible to establish sexual dimorphism, is recognisable in the mediterranean *Tropidoceras*. Therefore, we consider some of the specific names current in the literature to be refer in fact to these taxons.

We establish a detailed succession of Middle Carixian *Tropidoceras* species in the Mediterranean for the first time and correlate their associations with the biozonation established in Pliensbach.

We offer a hypothesis both about the origin of the genus in *Gemmellaroceras* and the evolution of the species within the genus, involving ontogenetic mechanisms of variation and retardation affecting the shell shape, ornamentation and suture line. The biogeographical distribution of the mediterranean species is largely restricted to the alpine cordilleras although individuals or populations occasionally reach the central and northern european basins. Certain mediterranean *Tropidoceras* reached the Pacific, probably by way of the "Atlantic seaway" and are to be found in sequences in Argentina, Alaska and Canada.

ZUSAMMENFASSUNG

In dieser Arbeit wird eine Revision der mediterranen Vertreter der Gattung *Tropidoceras* vorgenommen, ausgehend von dem reichen Material im Carixien der Betischen Kordilleren. Die untersuchten Exemplare stammen alle aus horizontierten Aufsammlungen am Nordrand des Subbetikums, obwohl Vertreter dieser Gattung auch aus anderen Profilen dieses Raumes bekannt sind.

Die Untersuchung ist von besonderem Interesse, da *Tropidoceras* im mittleren Carixien des Mediterrangebietes dominiert und die Biostratigraphie auf seinen Arten beruht. Die Häufigkeit und die Diversität des Materials erlauben eine taxonomisch-systematische Untersuchung, aufgrund deren die Gattung *Tropidoceras* zwischen die nahen Arten von *Gemmellaroceras* und *Acanthopleuroceras* gestellt werden kann.

Unter den mediterranen Vertretern der Gattung *Tropidoceras* werden sechs Morphospezien beschrieben (*T. erythraeum*, *T. demonense* – *T. flandrini*, *T. calliplocum* – *T. mediterraneum* und *T. zitteli* (Makro und Mikrokonch)).

Einige in der Literatur aufgeführten Arten werden als jüngere Synonyme der genannten Taxa angesehen.

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Zum ersten Mal wird für den Mittelmeerraum eine detaillierte Abfolge der Arten von *Tropidoceras* im mittleren Carixien beschrieben, und die Faunen werden mit der in der Typlokalität des Pliensbachian aufgestellten Zonengliederung korreliert.

Die Gattung *Tropidoceras* wird von *Gemmellaroceras* abgeleitet und die Evolution der zugehörigen Arten beschrieben. Diese Evolution impliziert Deviationsmechanismen und Retardation, die sowohl die Form des Gehäuses als auch die Skulptur und Lobenlinie betreffen.

Die biogeographische Verbreitung der mediterranen Arten ist grösstenteils auf den alpinen Raum beschränkt, wenn auch Individuen oder Vergesellschaftungen sporadisch auch die mittel- und nordeuropäischen Becken erreichten. Wahrscheinlich über die «via atlantica» erreichten einige mediterrane *Tropidoceras* den Pazifik und sind aus Serien in Argentinien, Kanada und Alaska bekannt.

Introduction

The *Tropidoceras* of the Betic Cordilleras are worth studying for the light they throw, not only on the classification of the Acanthopleuroceratinae, but also the paleo-biogeography of the Carixian.

There are many references to *Tropidoceras* in the Mediterranean (BREMER 1965, COLO 1961, DU DRESNAY 1963, FUCINI 1898, 1899, GÉCZY 1976, GEMMELLARO 1884, WIEDENMAYER 1977, 1980, etc.), but few studies deal with their taxonomy. This has necessitated the study of the genus, which has been possible thanks to its abundance in our region. *Tropidoceras* constitutes more than 50% of the ammonite fauna recorded in the subbetic Carixian, and its species form the basis of Middle Carixian biostratigraphy.

In the recent years, northern European *Tropidoceras*, together with other genera, have been described in works on Carixian ammonites (DOMMERGUES & MOUTERDE 1978,
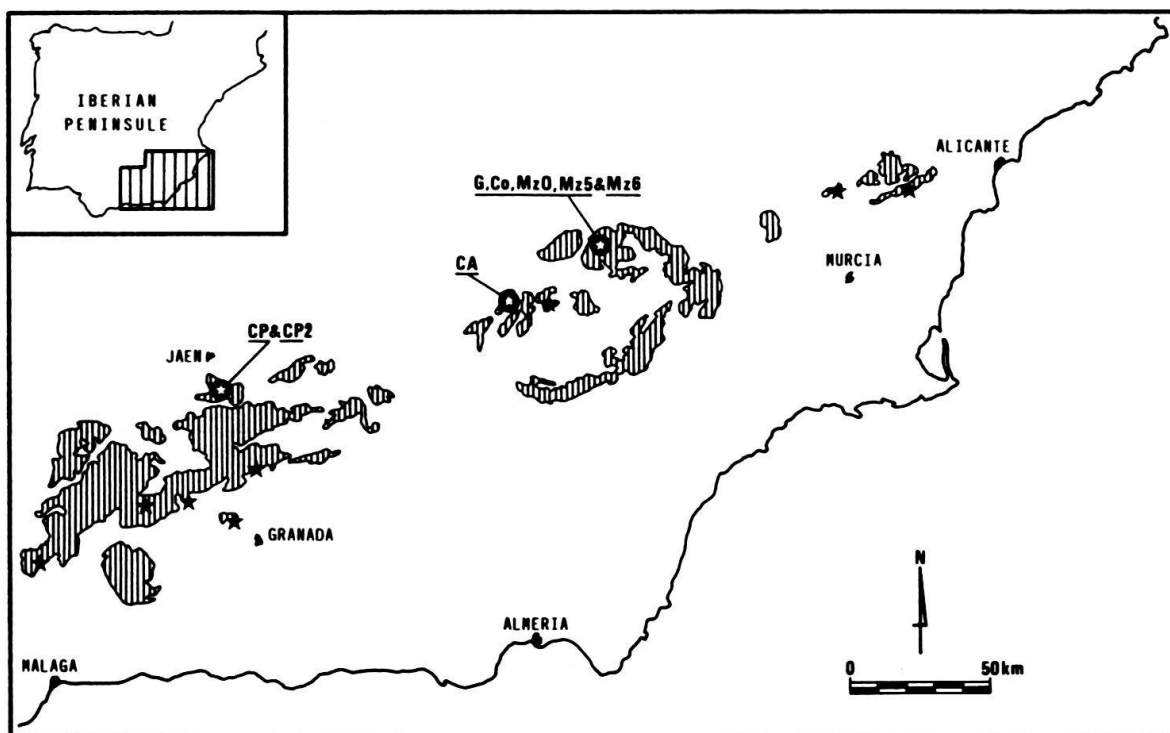

Fig. 1. Geographical and geological setting of the sequences *(shaded area)*: Mesozoic outcrops in the eastern and central parts of the Subbetic Zone (Betic Cordillera). CP: Cortijo Pilas; CP2: Cortijo Pilas 2; CA: Cueva del Agua; G: Garrumbre; CO: Cortijo Puerto Ortiz; MZO: Majarazan 0; MZ5: Majarazan 5; MZ6: Majarazan 6. *Black stars* other Subbetic sequences with *Tropidoceras.*

SCHLATTER 1980 etc.) so that a study of the Mediterranean forms has been necessary to improve our knowledge of the genus and its evolution.

The present study is based on a wealth of material, which has provided about 650 useable specimens of *Tropidoceras*. All the fossils studied are from the the northern edge of the Subbetic Zone, although *Tropidoceras* are also found in other parts of the basin (Fig. 1).

The Liassic sequences of the northern edge of the Subbetic Zone share a similar stratigraphic evolution. The Pre-Carixian Liassic consists of limestones with varied carbonate platform facies and containing remains of very diverse benthic organisms (cf. GARCIA HERNANDEZ et al. 1976, SEYFRIED 1978, BRAGA et al. 1982 etc.). These sediments change upwards, by way of "transitional facies", to marls and marly limestones, characteristic of the Middle to Upper Domerian and Toarcian.

The *Tropidoceras* samples come from the heterogeneous "transitional facies" (BRAGA et al. 1982) whose composition ranges from limonitic crusts to limonitic crusts associated with fossiliferous breccias, crinoidal biosparites, biomicrites or "red limestones" (SEYFRIED, op. cit.). Between these rock-types there are vertical and horizontal changes. Because of the quality and quantity of the fossil remains, the sampling in this case has been mainly in the facies of fossiliferous breccias, biosparites and biomicrites with cephalopods.

Because of the low sedimentation rate the sections are reduced or condensed and non-sequences are frequent. Consequently the sequence of biostratigraphical units represented and their thickness vary greatly from one section to another, even over distances of about 100 m (Fig. 2).

In the Carixian, the Subbetic basin became open to pelagic life forms with a correlative diversification of benthic faunas, which subsequently became impoverished in the overlying marly facies. The restricted living conditions of the organisms of the Lower Liassic carbonate platform gave way in the Carixian to a more open environment permitting cephalopods to become the predominant faunal elements. Pelagic conditions, however, did not come to prevail homogeneously throughout the basin and various facies are represented, reflecting this paleographical differentiation.

Because of the lithological characteristics already described, there are frequent outcrops, in which the faunas are disordered, lying without preferential orientation, at any angle to the bedding plane and with a high frequency of pre-fossilization shell fracture. This breakage has caused the differential preservation of small shells complete with body-chambers is more frequently in individuals of less than 50 mm in diameter. This means that in larger forms the body-chamber and the phragmocone have usually been fossilized separately.

The oblique orientation of the shells to the bedding planes has resulted in their deformation in all directions rather than the more usual deformation only affecting the thickness.

The specimens studied are mostly limestone moulds, some of them with the remains of transformed shell. The innermost part of the phragmocones are usually filled with calcite. This type of fossilization and the relatively coarse-grained sedimentation has meant a frequent loss of fine detail in the ornamentation of the *Tropidoceras* collected.

Despite these general conditions prevailing in most of the sections, the Cueva del Agua (CA) sequence is thicker, fossil breakage is minimal and the fossils lie parallel to the
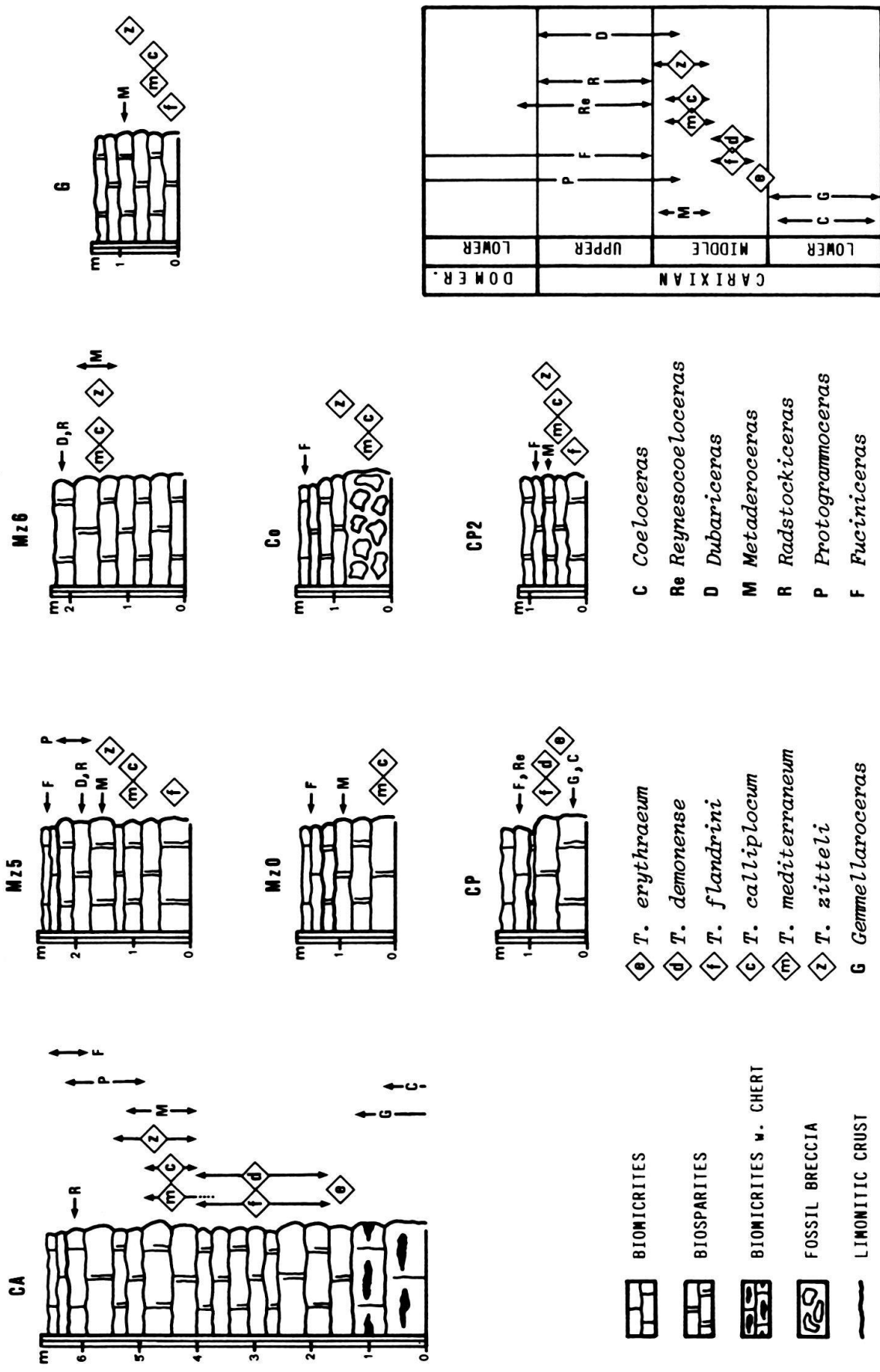
Fig. 2. Sequences and biostratigraphical distribution of the *Tropidoceras* species and the other important genera found in the Subbetic Carixian (locality symbols as in Fig. 1).

bedding planes. In this sequence a given *Tropidoceras* morphology may have a vertical range of the order of 1 m and extend through several strata. For these reasons we have chosen the outcrop as the type-sequence for the vertical distribution of the species studied and their temporal relationships.

Systematic Paleontology

Superfamily *Eoderocerataceae* SPATH 1929

Family *Polymorphitidae* HAUG 1887

Subfamily *Acanthopleuroceratinae* ARKELL 1950

Genus *Tropidoceras* HYATT 1867

Type species (subsequently designated by HAUG 1885): *Ammonites masseanus* D'ORBIGNY 1848

Following BREMER's description (1965), *Tropidoceras* includes relatively evolute, compressed forms, with a narrow ventral region, sharp keel, smooth to feeble ribbing, and a deeply divided suture line. ARKELL (1957) and GÉCZY (1976) add the presence of secondary and/or residual ribs in the ventrolateral part of the whorl-side.

Tropidoceras lies morphologically and chronologically between *Gemmellaroceras* and *Acanthopleuroceras* and, in spite of the definition already quoted, there are problems in the generic attribution of borderline *Tropidoceras* species morphologically close to the other two genera.

Gemmellaroceras are usually smaller than *Tropidoceras* and lack a keel. Nevertheless, *G. alloplocum* (GEMM.) has either a poorly developed keel or a very angular venter. *T. erythraeum* (GEMM.), which is very similarly ornamented and is chronologically the nearest *Tropidoceras*, is distinguished from it mainly by the clear development of the keel from an early ontogenetic stage.

Acanthopleuroceras is generally distinguished from *Tropidoceras* by its polygonal section (rectangular, pentagonal, etc.), a less developed keel, straight strong ribbing with one or two rows of pronounced tubercles and simpler suture line.

In spite of this general differentiation, transitional forms exist (GÉCZY 1976, DOMMERGUES & MOUTERDE 1978 etc.), in particular *Ammonits stahli* OPPEL, which has been assigned to both genera in the last sixty years. In our view, it belongs morphologically to *Tropidoceras*, since it has no important characteristics to differentiate it from the most typical species of that genus, and has residual and secondary ribs (more obvious in adult specimens) in the outer part of the flank, which are typical of *Tropidoceras* (SCHLATTER 1980).

The suture line of *Ammonites stahli* has a lateral lobe with characteristics intermediate between *Tropidoceras* and *Acanthopleuroceras* as occur in the subbetic *Tropidoceras zitteli*. In some specimens of this *Tropidoceras* species the lateral lobe tends to be bifid, as in *Tropidoceras*, while yet in others the tendency is towards an ill-defined trifidism, characteristic of *Acanthopleuroceras*.

DOMMERGUES & MOUTERDE (1978), considering the suture lines of the *Tropidoceras–Acanthopleuroceras* group of the Middle Carixian of Cottards, ascribe a lineage by way of *Tropidoceras* sp., to *Acanthopleuroceras*, different from that of *Ammonites stahli*, which

they include with reservations in the genus *Tropidoceras*. For this reason, it appears pointless to use the at best equivocal evidence presented by their suture lines, to include *Ammonites stahli* in the genus *Acanthopleuroceras*.

VENTURI (1978) has proposed the generic name *Catriceras* for his species *C. catriense*, whose morphology is close to that of *T. stahli*. According to him, the morphological differences between the two species are a more compressed section, a flatter ventral region, less developed tubercles, a greater curvature of the ribbing, a less developed U_2 lobe and accessory lobe of the external saddle in *C. catriense*.

Its morphology might warrant the inclusion of *T. stahli* in *Catriceras*, but the biostratigraphical position of that genus, i.e. of the species *C. catriense*, and its relationship with other forms of *Tropidoceras* and *Acanthopleuroceras* are imprecise. Consequently, for the moment at least, the use of VENTURI's term would only confuse the classification of the Acanthopleuroceratinae without adding anything worthwhile.

Tropidoceras flandrini (DUMORTIER 1869)

1868   *Ammonites Flandrini* DUMORTIER, p. 72, Pl. 14, Fig. 1–2.
1884   *Harpoceras zancleanum* GEMMELLARO, p. 38, Pl. 5, Fig. 5–9.
1899   *Tropidoceras Flandrini* DUM.; FUCINI, p. 168, Pl. 23, Fig. 2.
?1965   *Tropidoceras masseanum galatense* (GEMMELLARO); BREMER, p. 187, Fig. 2d.
?1965   *Tropidoceras ellipticum demonense* (GEMMELLARO); BREMER, p. 188, Fig. 2a.
1976   *Tropidoceras* cf. *flandrini* (DUMORTIER); GÉCZY, p. 92, Pl. 17, Fig. 8–9.
1977   *Tropidoceras flandrini densicosta* (FUTTERER); WIEDENMAYER, p. 64, Pl. 4, Fig. 1–2.

Holotype. – DUMORTIER 1869, Plate 14, Figure 1, 2 (Dumortier Collection, Natural History Museum of Lyon).

Material. – 81 specimens.

Description. – These are large forms of medium whorl expansion rate, elliptical in section with flattened whorl sides. The ventral region carries a keel flanked by two narrow fillets inclined towards the sides of the shell.

The shell is slightly allometric, indicating an acceleration in whorl expansion, both in height and thickness, which becomes obvious at a diameter of 90–100 mm. There are no great variations in shell shape between individuals attributed to the species (see Fig. 3), and none of the parametric relations shows variation exceeding 10% in any diameter.

The ornamentation begins with weak, barely sinuous, slightly rursiradiate ribs, flattened on the outer part of the whorl side. This ribbing gradually gives way to barely sigmoid, slightly retroverse ribs, which, at ⅔ of the height of the flank, branch into 2–4 secondaries with faint intercalatories, describing a gentle curve towards the aperture in the outermost part of the flank. The ribs may be sharpened at the umbilical edge and/or at the point of bifurcation and, in certain individuals, form a true tubercle. The body chamber is similary ornamented with more pronounced sharpenings and/or tubercles. There is a notable variation between individuals belonging to a single level, ranging from specimens in which the tubercles are barely perceptible, to others in which they are very pronounced, with every intermediate stage represented. The diameter at which they become evident (if they are present) also varies greatly.

In adult specimens, the suture is strongly indented with a characteristic external saddle and lateral lobe. The external saddle is broad and asymmetrically divided by a trifid central lobe. The external lobe is bifurcate and very complicated with four second
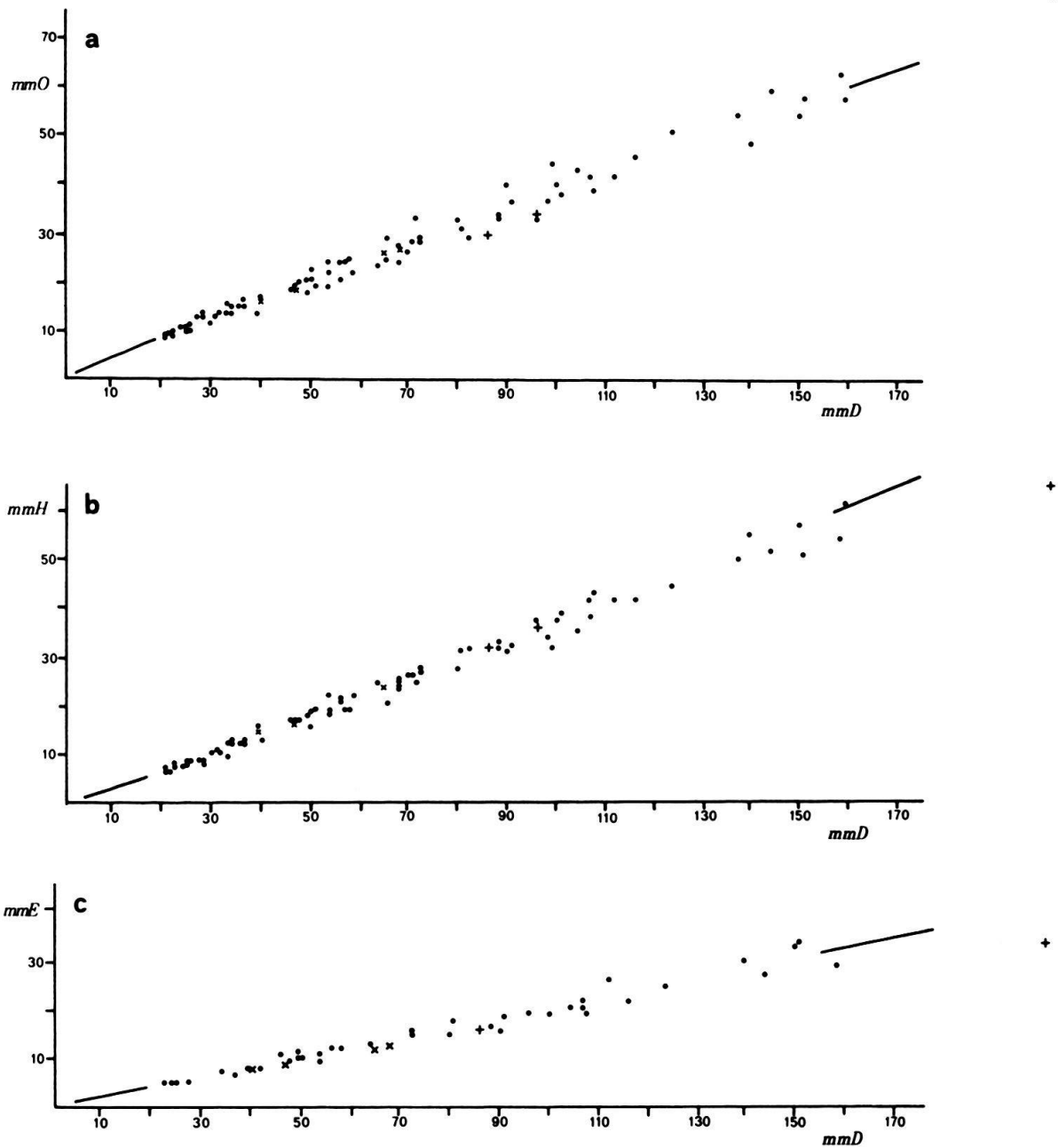
Fig. 3. *T.flandrini.* Whorl parameters diagrams: a) D/O, b) D/H, c) D/E. D: diameter; E: whorl width; O: umbilical diameter; H: whorl height. + holotype of *T.flandrini* (DUMORTIER 1869, Pl. 14, Fig. 1, 2). × sintypes of "*H.zancleanum*" (GEMMELLARO 1884, Pl. 5, Fig. 5–9).

ary lobes, which in turn are bifid or trifid. The umbilical lobes are much smaller and generally trifid.

Observations. – We believe that the specimens which GEMMELLARO (op.cit.) identifies as "*Harpoceras*" *zancleanum* are in fact either the internal whorls or immature individuals of *T.flandrini.* The forms he illustrates are morphologically indistinguishable from the early whorls of our subbetic specimens and their shell dimensions fall within the range of those of *T.flandrini.* It is also worth bearing in mind that the specimen found in the same

formation (?), which he identifies as *T. flandrini,* is a fragment of a considerably larger individual.

The WIEDENMAYER's neotype of *T. flandrini* var. *densicosta* is difficult to distinguish from *T. flandrini* (s.str.). The morphological differences he quotes for the *densicosta* variety (higher whorl-side, smaller umbilicus, less developed tubercles and sharper ventral region), are actually imperceptible within the variability observed in a sample of several *T. flandrini* from the same level of a single subbetic outcrop (i.e. bed 4s of the CP sequence). Nevertheless, *T. flandrini densicosta* illustred by SCHLATTER (1980) and the specimen illustrated by FUTTERER (1893) both coming from South German sequences, show a morphology which is outside the range observed in our sample of the species.

T. flandrini var. *semilaevis* FUCINI (1899, p. 169, Pl.22, Fig. 1) represents a very singular morphology, feebly ornamented and with no complicated suture line (FUCINI, 1899, Text-Fig. 15). As similar morphologies have not been recorded in the Subbetic Zone, it is difficult to interprete the specimen of *T. flandrini semilaevis* illustred by FUCINI, but it could possibly be an anomalous specimen of *T. flandrini.*

The most typical characteristic of *T. flandrini* and *T. demonense* is the flattening of the whorl-sides, at least of the inner whorls. It is distinguishable from *T. zitteli* by its numerous intercalated ribs. The ribs of *T. mediterraneum* on the other hand, are clearly sigmoid and prorsiradiate.

Tropidoceras demonense (GEMMELLARO 1884)

1884 *Harpoceras Demonense* GEMMELLARO, p. 41, Pl. 7, Fig. 1–5, ?6, ?7, 8 and 9.
1896 *Tropidoceras Demonense* GEMM.; FUCINI, p. 248, Pl. 25, Fig. 24.
1963 *Tropidoceras demonense* (GEMMELLARO); DU DRESNAY, p. 151, Pl 2, Fig. 7.
1968 *Tropidoceras demonense* (GEMMELLARO); CANTALUPPI & MONTANARI, p. 73, Pl. 13, Fig. 2.
1973 *Tropidoceras demonense* (GEMM.); LINARES & RIVAS, Pl. 1, Fig. 1, 3, 4.
1973 *Tropidoceras galatense* (GEMM.); LINARES & RIVAS, Pl. 1, Fig. 2.
1976 *Tropidoceras ellipticum demonense* (GEMMELLARO); GÉCZY, p. 76, Pl. 17, Fig. 3.
1976 *Tropidoceras ellipticum* (SOWERBY); GÉCZY, p. 76, Pl. 17, Fig. 2.
1976 *Tropidoceras* aff. *galatense lineatum* SPATH; GÉCZY, p. 88, Pl. 17, Fig. 4.

Lectotype: – GEMMELLARO 1884, Plate 7, Fig. 1, 2, 8 (BREMER 1965, p. 188), kept in the Museo di Geologia e Paleontologia of Palermo University.

Material. – 35 specimens.

Description. – These are forms of medium size and whorl expansion rate, elliptical in section with flattened whorl sides. The venter is sharp with a keel flanked by two narrow smooth areas inclined towards the whorl-sides. In the sample shown in Figure 4, the correlation between the shell parameters is very high. As in other species, the greatest variations are in whorl thickness, which is largely caused by the different materials in which the various specimens are preserved.

The ornamentation, which tends to be weak, consists of slightly sigmoid, rounded, ribs. These are slightly rursiradiate and markedly weaker at the shoulder, where they become projected. The lack of ornamentation is even more marked in the body chamber, where the ribs become barely perceptible and are reduced to striae, some dividing into two or three near the shoulder.

The suture is similar to, but not as indented as that of the adult *T. flandrini.* Juvenile *T. demonense* have a relatively larger U_2 than adult specimens.
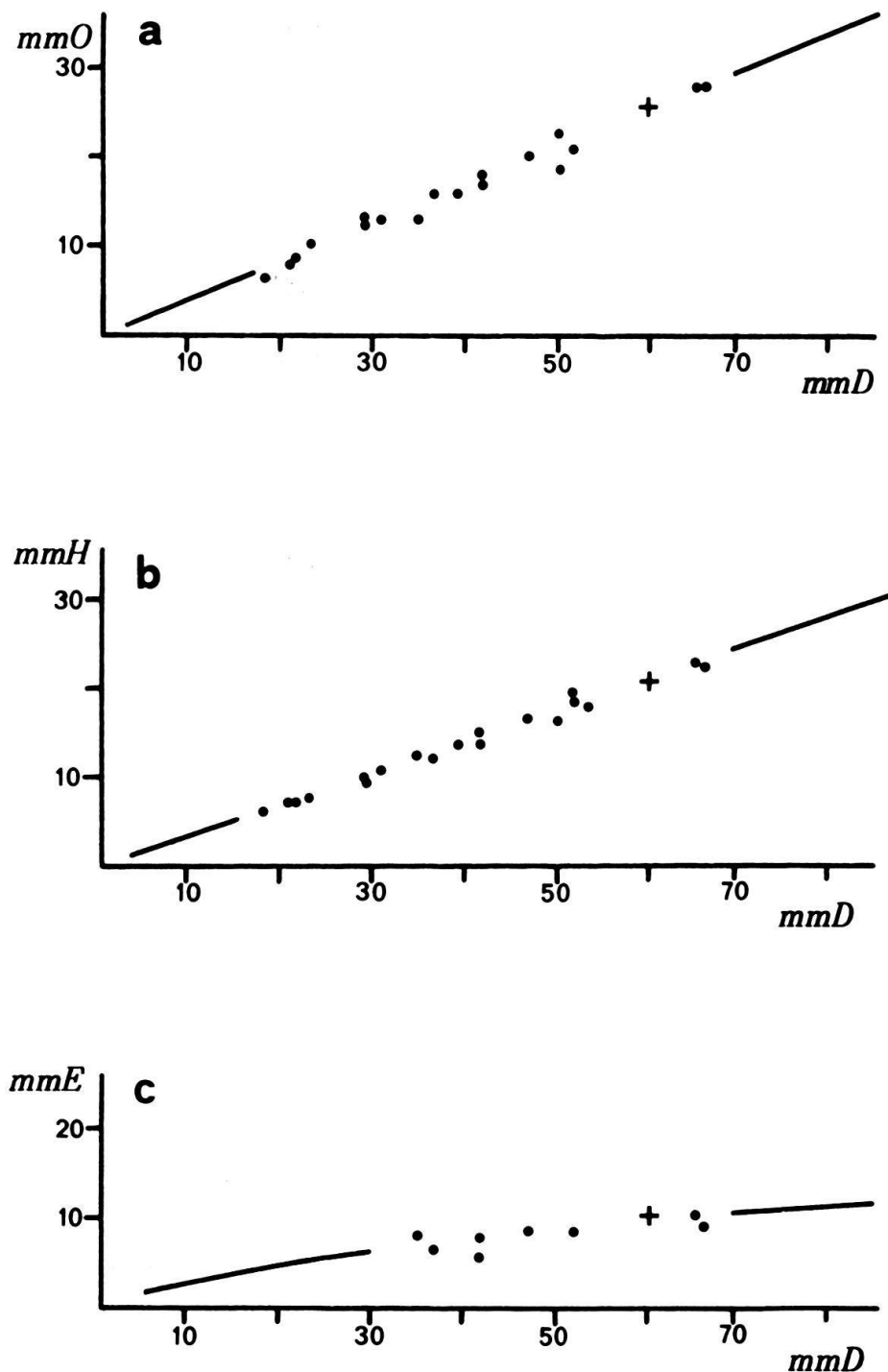
Fig. 4. *T. demonense*. Whorl parameters diagrams: a) D/O, b) D/H, c) D/E. + lectotype of *T. demonense* (GEMMELLARO 1884, Pl. 7, Fig. 1, 2, 8).

Observations. – The shell morphology and its variability in this species and *T. flandrini* are similar at comparable diameters (see Fig. 3 and 4). Fully developed *T. demonense* resemble *T. flandrini* up to 70–80 mm, and the species cannot be clearly distinguished at these stages by either shell shape or suture. There are only slight differences in ornamentation, that of *T. flandrini* tending to be more marked at similar diameters. Also the whorl thickness of *T. demonense* reaches values lower than in *T. flandrini*.

Tropidoceras erythraeum (Gemmellaro 1884)

1884   *Harpoceras erythraeum* Gemmellaro, p. 40, Pl. 5, Fig. 10–16.
1896   *Tropidoceras erythraeum* (Gemmellaro); Fucini, p. 248, Pl. 25, Fig. 22.
1965   *Tropidoceras erythraeum* (Gemmellaro); Bremer, p. 187, Fig. 2c.
?1976 *Gemmellaroceras* sp.; Géczy, p. 75, Pl. 14, Fig. 8.

Lectotype: – Gemmellaro 1884, Plate 5, Figure 10, 11 (Bremer 1965, p.187). In the Museo di Geologia e Paleontologia of Palermo University.

Material: – 5 specimens.

Observations. – Gemmellaro's "*H. erythraeum*" fits perfectly within the range of variability observed in subbetic *T. demonense*. Its weak ornamentation, with irregular rounded ribs, resembles that of the latter species, although *T. erythraeum* (Gemmellaro) seems also to include forms of thicker section and even weaker ribbing. This observation fits in with the allometry observed in *T. demonense,* in which the section widens faster in the early stages (up to 30–40 mm in diameter), since the samples attributed to *T. erythraeum* and its syntypes (Gemmellaro 1884, Pl. 5, Fig. 1–16) are all small.

Nevertheless *T. erythraeum* appears biostratigraphically little before typical *T. demonense,* and it have been never found associated to *T. flandrini.*

Its simple ontogenetic development and weak ornamentation result in a marked similarity between this and the juvenile forms of other taxa described in the literature, e.g. the difficulty in distinguishing if from *T. ellipticum,* whose supposed holotype (cf. Spath 1928) is a nucleus of an ammonite with poorly marked ornamentation. A similar case is that of *T. lineatum* Spath, illustrated by a small exemplar (Spath 1928, Pl. 6, Fig. 3; only phragmocone) with incipient ornamentation.

Tropidoceras mediterraneum (Gemmellaro 1884)

1884   *Hapoceras Masseanum* D'Orb. var. *mediterranea* Gemmellaro, p. 36, Pl. 5, Fig. 1–4.
1884   *Harpoceras Galatense* Gemmellaro, p. 43, Pl. 4, Fig. 15–23.
1936   *Tropidoceras (Cycloceras) masseanum* D'Orb. var. *mediterranea* Gemm.; Termier, p. 1270, Pl. 20, Fig. 1.
1963   *Tropidoceras masseanum* (D'Orbigny) var. *mediterraneum* Gemmellaro; Du Dresnay, p. 150, Pl. 2, Fig. 6.
1966   *Tropidoceras masseanum* (D'Orbigny); Kollarova-Andrusova, p. 49, Pl. 14, Fig. 3.
1977   *Tropidoceras masseanum* (D'Orbigny); Wiedenmayer, p. 62, Pl. 12, Fig. 13, Pl. 13, Fig. 8.

Lectotype. – Gemmellaro 1884, Plate 5, Figure 1. In the Museo di Geologia e Paleontologia of Palermo University. Here scelted.

Material. – 112 specimens.

Description. – These are large forms. Whorl expansion rate is moderate in the first whorls and increases slightly thereafter. Samples from the same site show an excellent correlation between the shell dimensions. Samples of different provenance show a greater variation, though this never exceeds 7% for a given diameter. They are of oval section with a sharp, highly keeled venter.

The ornamentation consists of sigmoid prorsiradiate ribs. Their sharpness and density vary from individual to individual. At $\frac{3}{5}$ of the whorl height, the lateral ribs branch into 2–4 less strongly marked secondaries interspersed with residual intercalated ribs, all peripherally projected.

This intercalation is sporadic in the first whorls. Rib division diminishes on the body chamber of adult specimens, where most ribs remain simple and better defined. The
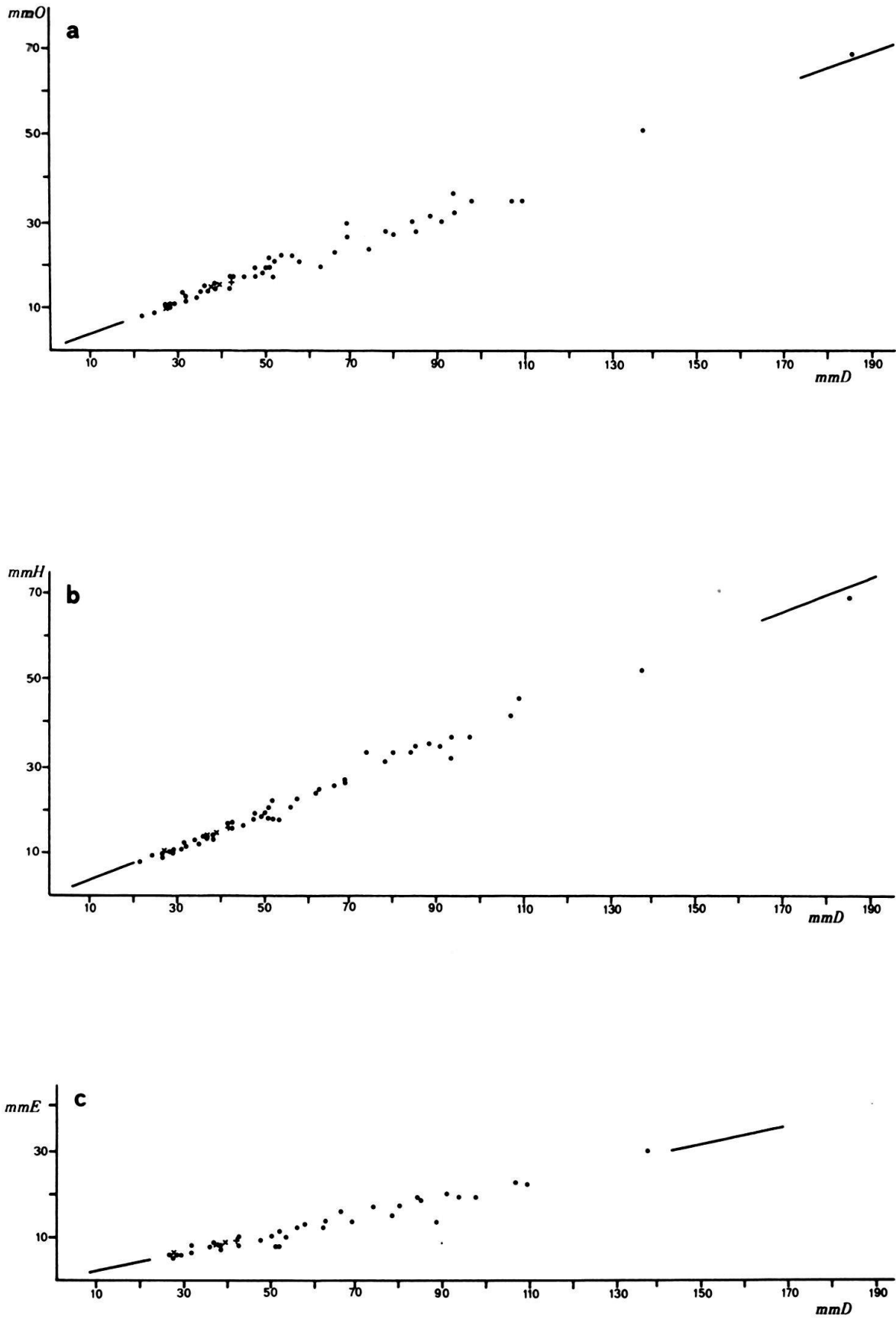
Fig. 5. *T. mediterraneum.* Whorl parameters diagrams: a) D/O, b) D/H, c) D/E. + sintype of *T. mediterraneum* (GEMMELLARO 1884, Pl. 5, Fig. 1). × sintypes of *"H. galatense"* (GEMMELLARO 1884, measured by this author).

suture is less indented than that of other large forms of the genus and, in general, resembles that of *T. calliplocum*. It is also similar to that of juvenile specimens of *T. demonense*, although the lateral lobe is more open, especially in the adult sutures.

Observations. – The set of specimens GEMMELLARO called *"H."galatense* may be interpreted as fragments of *T. mediterraneum*, in which only the first whorls are preserved, or possibly as immature specimens. The similarity is evident between the *"H."galatense* syntypes and *"H."masseanum* var. *mediterranea* "whose external whorls have been lost", as quoted by GEMMELLARO (1884).

We have chosen the specific name *T. mediterraneum*, originally given to a variety, instead of *T. galatense*, because the ontogenetic development of its types has been better illustrated. GEMMELLARO, as we have seen considers this species to be a variety of *T. masseanum* D'ORBIGNY, as do most subsequent authors, some of whom even identify *T. masseanum* completely with *T. mediterraneum* (except COLO 1961; DU DRESNAY 1963). The two species differ, however, in that the whorl expansion of *T. masseanum* is slower, its ornamentation stronger and coarser, while the section of *T. mediterraneum* is more ogival.

Tropidoceras calliplocum (GEMMELLARO 1884)

1856	*Ammonites Actaeon* D'ORB.; HAUER, p. 31, Pl. 9, Fig. 4–8.	
1884	*Harpoceras calliplocum* GEMMELLARO, p. 44, Pl. 7, Fig. 11–18.	
?1896	*Cycloceras Actaeon* (D'ORB.); PARONA, p. 31, Pl. 2, Fig. 8.	
1896	*Tropidoceras calliplocum* GEMM.; FUCINI, p. 247, Pl. 25, Fig. 25.	
1899	*Tropidoceras Stefanii* FUCINI, p.172, Pl. 5, Fig. 3.	
1899	*Cycloceras calliplocum* GEMMELLARO; HUG, p. 31, Pl. 8, Fig. 4.	
1965	*Tropidoceras calliplocum* (GEMMELLARO); BREMER, p. 189, Fig. 2b.	
1965	*Tropidoceras actaeon orientale* BREMER, p. 189, Pl. 6, Fig. 9.	
1976	*Tropidoceras actaeon calliplocum* (GEMMELLARO); GÉCZY, p. 85, Pl. 18, Fig. 1; Pl. 17, Fig. 1(?).	

Lectotype. – GEMMELLARO 1884, Plate 7, Figure 11 (SPATH 1928, p.228). In the Museo di Geologia e Paleontologia of Palermo University.

Material. – 217 specimens.

Description. – These are forms of medium size and whorl expansion rate, which is constant throughout their development. Their section is elliptical and the sharp venter has a keel with two fillets tilted towards the whorl sides. The ornamentation consists of sigmoid ribs, varying considerably in strength and density between specimens. They are slightly rursiradiate, with a gentle peripherical projection, in which the ribs occasionally branch into two, or intercalated ribs appear. The ornamentation hardly changes on the body chamber, although the number of secondary and intercalated ribs increases.

Observations. – Although *T. calliplocum* abounds in the Carixian of the Subbetic Zone it is hardly mentioned in the literature, probably because it is restricted to the Tethyan Realm, whose Pliensbachian faunas have been little studied. Like *T. demonense*, it resembles many species of *Tropidoceras* and *Acanthopleuroceras*, especially internal whorls and fragmentary specimens, mainly because of its very simple ornamentation and ontogenetic development. The ornamentation is similar to that of various specimens of *T. demonense*, but is stronger and more sharply defined and its section is never as compressed.

Generally speaking, there is a great similarity between *T. calliplocum* and many of the "species" described by SPATH (1928, *T. lineatum*, *T. sparsicosta* and *T. futtereri*). These
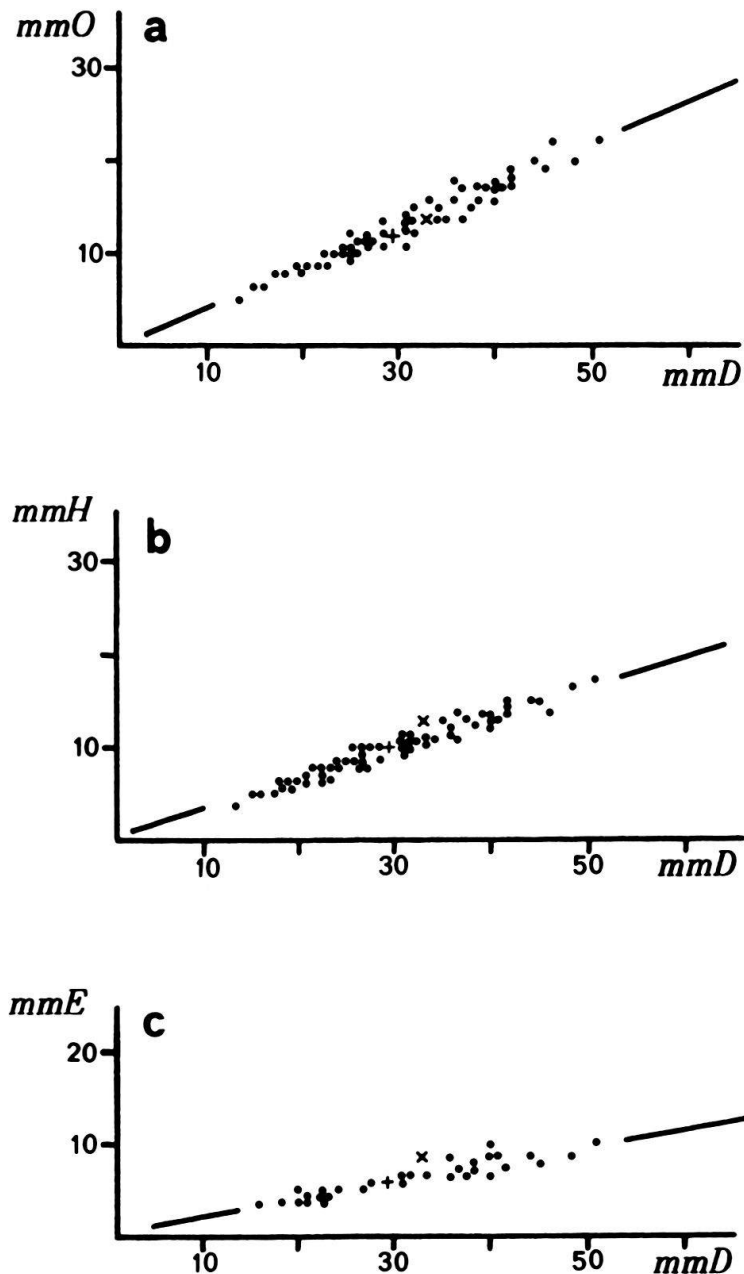
Fig. 6. *T.calliplocum*. Whorl parameter diagrams: a) D/O, b) D/H, c) D/E. + holotype of *T.actaeon orientale* (BREMER 1965, Pl. 16, Fig. 9). × A sintype of *T. calliplocum* (GEMMELLARO 1884, measured by this author).

show a great likeness to each other and are difficult to distinguish from some of the juvenile forms of *T. masseanum* (cf. DOMMERGUES & MOUTERDE 1978).

On the other hand, we can find no morphological criterion to distinguish this species from BREMER's (1965) *T. actaeon orientale* (holotype), whose ornamentation and shell structure are characteristic of *T. calliplocum*. After DOMMERGUES & MOUTERDE (op.cit.) oblige us to consider *A. actaeon* as a true *Acanthopleuroceras,* appearing high within the biostratigraphic range of the genus, far from the last *Tropidoceras*. In general, most of the "*T. actaeon*" cited in the Tethyan Realm probably belong to *T. calliplocum*.

T. stefanii FUCINI is indistinguishable from *T. calliplocum,* especially, if we compare it with the specimens with the less developed ornamentation of *T. calliplocum*.

Tropidoceras campiliense FUCINI, known only from the holotype (FUCINI 1898, p. 248, Pl. 20, Fig. 6) seems to be a probably aberrant specimen of *T. calliplocum*. The shell morphology ontogeny and elements of the suture line correspond to those of large specimens of *T. calliplocum*. The asymmetrical character of the suture line, added to the singularity of the morphology within the mediterranean *Tropidoceras* point to it as an anomalous specimen rather than the existence of an independent species.

Tropidoceras zitteli FUCINI 1899

1899   *Tropidoceras Zitteli* FUCINI, p. 170, Pl. 22, Fig. 3.
1899   *Cycloceras Stahli* OPPEL; FUCINI, p. 173, Pl. 22, Fig. 2.
1927   *Acanthopleuroceras Stahli* OPP.; SCHROEDER, p. 4, Pl. 13, Fig. 8.
1976   *Tropidoceras zitteli* FUCINI; GÉCZY, p. 91, Pl. 17, Fig. 7.
1976   *Acanthopleuroceras stahli* (OPPEL); GÉCZY, p. 95, Pl. 18, Fig. 4–6.
1976   *Acanthopleuroceras subarietiforme* (FUTTERER); GÉCZY, p. 94, Pl. 18, Fig. 3.
?1976 *Acanthopleuroceras* cf. *maugenesti* (D'ORBIGNY); GÉCZY, p. 97, Pl. 18, Fig. 8.
1977   *Tropidoceras stahli* (OPPEL); WIEDENMAYER, p. 65, Pl. 14, Fig. 3–11.

Holotype. – FUCINI 1899, Plate 22, Figure 3. The specimen comes from Monte Primo. Deposited in Museo di Pisa.

Material. – 193 specimens.

Description. – These are forms of relatively slow whorl expansion compared with the rest of the genus. The section ranges from elliptical to rectangular. The ventral region is compressed, with a keel flanked by two fillets inclined towards the whorl sides, perpendicular to the keel or depressed, forming grooves according to ontogenetic development and varying from specimen to specimen.

The ornamentation is strong, made up of rursiradiate ribs from almost straight to slighly sigmoidal on the flanks. These thicken at the umbilical and the ventral margins and their height decreases sharply as they project forward. At this point sporadic intercalated ribs may occur.

The suture differs from the other *Tropidoceras* which have been described. The morphology of the lateral lobe varies in even the earliest specimens. In general, it tends to be trifid, and longer and narrower than in other *Tropidoceras* species. There are, nevertheless, examples in which it is still clearly bifid. The U_2 lobe is relatively large and the external saddle is very broad, and divided in two more symmetrically than in the *Tropidoceras* already described.

Within the range of *T. zitteli* we may distinguish two groups by their size, whorl expansion rate and, above all, by the thickness and strength of ornamentation in adult specimens. The increase in whorl height is similar in both groups, although it tends to be a little slower in smaller specimens, with an even slower growth in whorl width.

Observations. – *T. zitteli* is the only *Tropidoceras* in the upper strata of the subbetic Middle Carixian already studied. Within this species at these levels we find a relatively great variability in shell morphology in specimens of more than 50 mm in diameter. This range includes specimens with ornamentation characteristics of the typical *T. zitteli*. The same levels have furnished many forms with fillets slightly inclined toward the whorl side, and others with grooves in the venter, as well as intermediate forms between these extreme morphologies. This transition is also to be found at various stages in the development of certain specimens, in which the ventral grooves appear and disapear
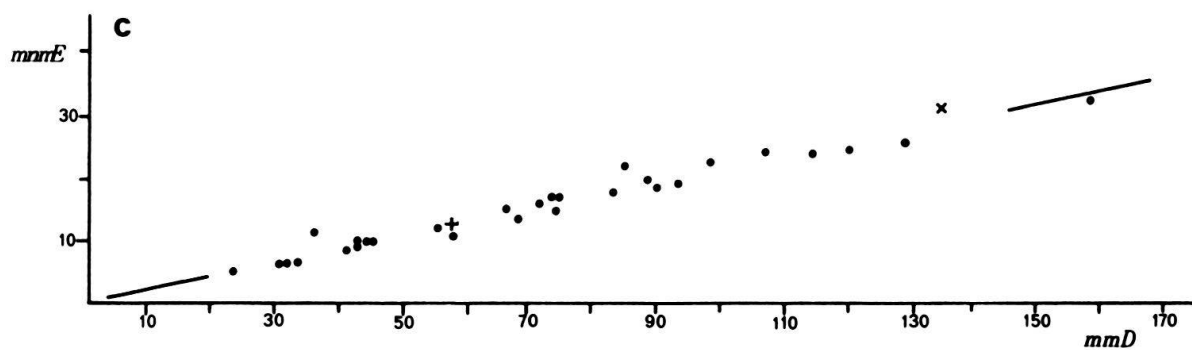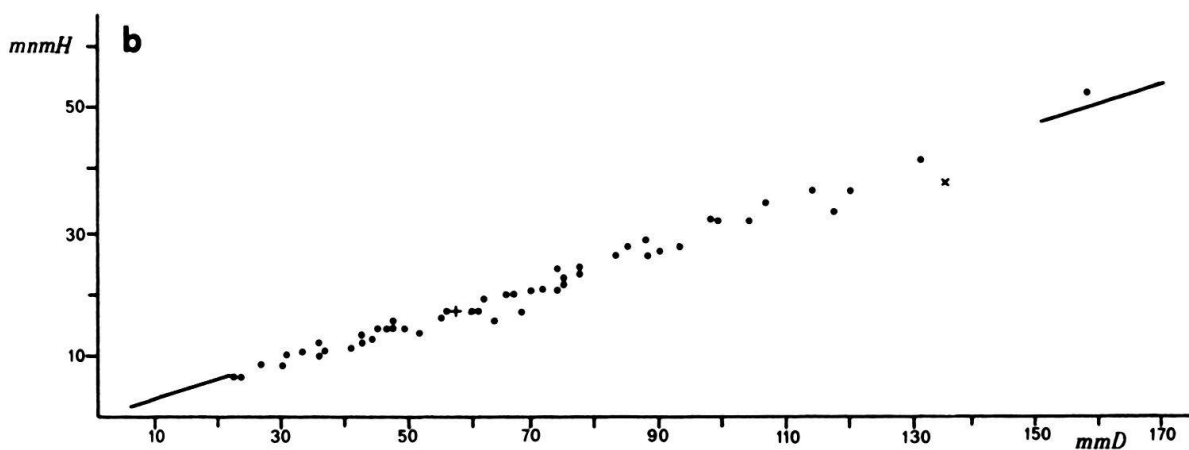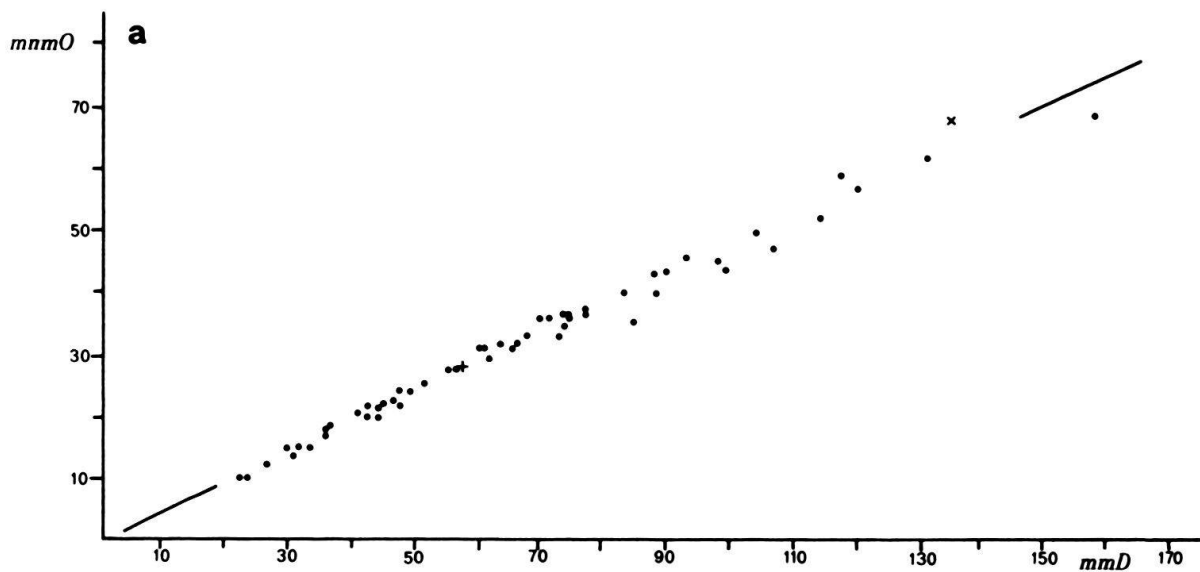
Fig. 7. *T. zitteli* Macroconch. Whorl parameter diagrams: a) D/O, b) D/H, c) D/E. + holotype of *T. stahli* (OPPEL 1853, Pl. 3, Fig. 2). × holotype *T. zitteli* (FUCINI 1899, Pl. 22, Fig. 3).
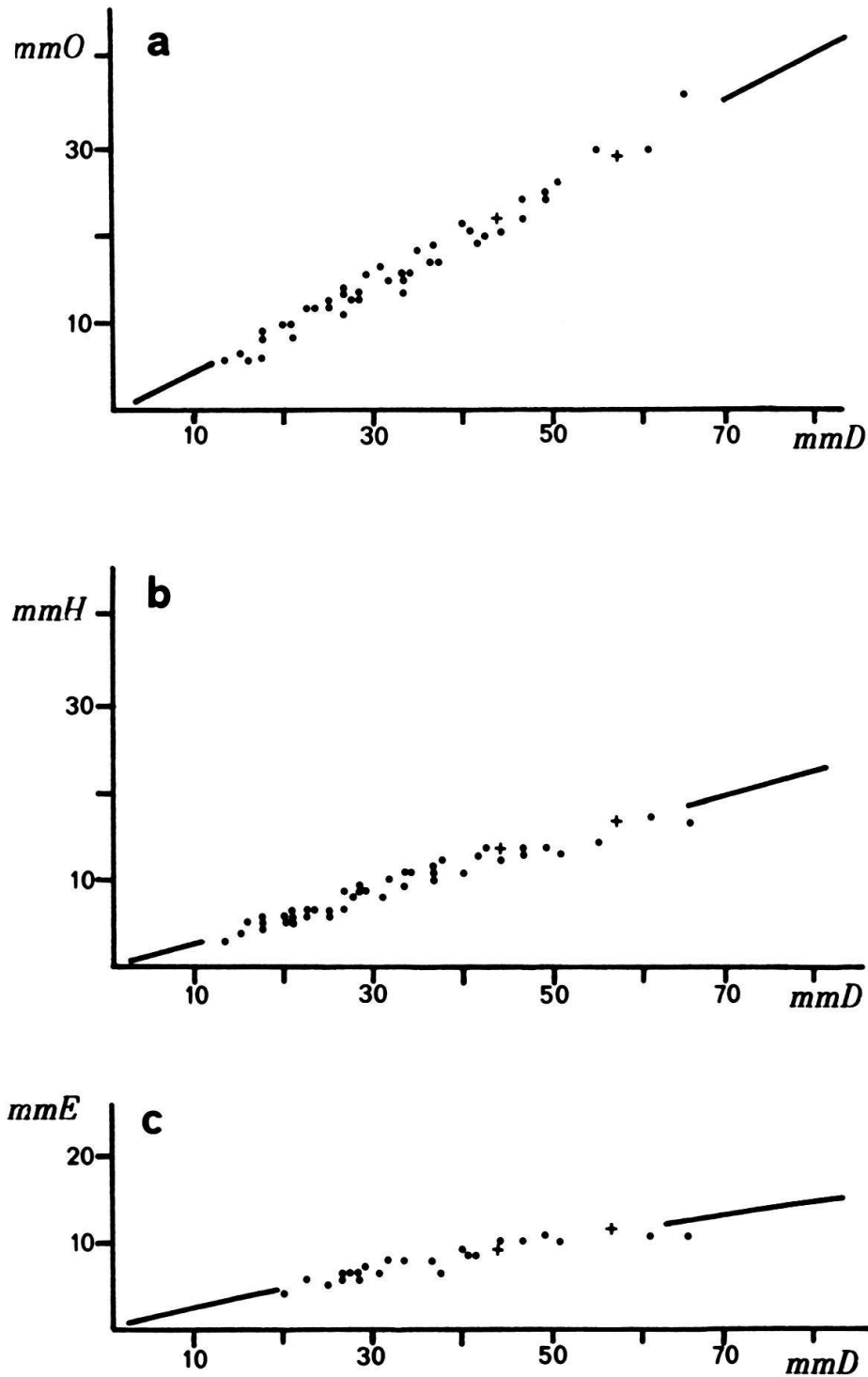
Fig. 8. *T. zitteli* Microconch. Whorl parameter diagrams: a) D/O, b) D/H, c) D/E. + holotype of *T. stahli* (OPPEL 1853, Pl. 3, Fig. 2).

gradually. The individuals with ventral grooves and relatively low ribbing density are close to *"T."subarietiforme*. The suture line of this centroeuropean species shows strong similarities with that of subbetic *T. zitteli* (see SCHLATTER 1980, Fig. 23c and d).

The subbetic forms studied here as *T. zitteli* have been considered until now as *T. stahli,* as have other similar exemplars from other mediterranean regions.

The morphology of the *T.stahli* type (OPPEL 1853, Pl.3, Fig.2a–b; incomplete specimen) resembles that of the internal whorls of the small exemplars of *T.zitteli*. *T.stahli*, however, as illustrated in SCHLATTER (1980), differs a little in the ornamentation of its adult structure and body chamber from our subbetic specimens, above all, in having well defined secondary ribs. These morphological differences can be seen clearly in the exemplar of *T.stahli*, which QUENSTEDT (1885, Pl.36, Fig.12) considered to be *A.masseanus*.

Given these differences, we prefer to classify the subbetic forms as *T.zitteli*, despite the fact that so slight they may reflect nothing more than geographical differentiation within the same biospecies. It is, of course, also possible that they only represent the degree of preservation allowed by the materials, in which they have been fossilized.

Although *A.gigas* (QUENSTEDT) (well illustrated by SCHLATTER, op. cit. Pl.18, Fig.1) shows a shell morphology and ribbing similar to those of large adults of subbetic *T.zitteli*, the suture line (see lectotype in QUENSTEDT 1885, Pl.35, Fig.14) has clear *Acanthopleuroceras* characteristics (trifid lateral lobe).

Ammonites arietiformis OPPEL, ascribed to *Tropidoceras* or *Acanthopleuroceras*, by northern European authors has characteristics similar to those of the more developed forms found in our sequences, but their fastigate section, typical of *Acanthopleuroceras*, does not appear in any forms found in the Subbetic Zone.

DOMMERGUES (1984) points out that many of the mediterranean *Tropidoceras* included in *T.stahli* by different authors, may well correspond to *C.catriense*. As we have already specified in the generic discussion, the type of *C.catriense* has no clearly defined biostratigraphic position. The specimens of FERRETTI coming from Monte Catria, quoted by DOMMERGUES (op.cit.) have the same association than *T.zitteli* in the Subbetic Zone; Moreover, we consider the specimens illustrated by WIEDENMAYER (1977, Pl.14, Fig.5–8) and GÉCZY (1976, Pl.18, Fig.4–6) attributed by DOMMERGUES to *T.catriense* to be *T.zitteli*. Finally we prefer to reserve judgement on *C.catriense* for want of adequate biostratigraphical definition.

Biochronology and faunal succession

In the Subbetic Zone, ammonites are rare in early Carixian sequences, in which only a few *Gemmellaroceras*, "*Miltoceras*", *Coeloceras*, etc. have been found. The earliest *Tropidoceras* (*T.erythraeum* morphology) appear in association with the last *Gemmellaroceras* and *Coeloceras*.

The first morphologically well-defined *Tropidoceras*; *T.demonense* and *T.flandrini*, have been found after the disappearance of *Gemmellaroceras*. They are the only ammonite species found in these parts of the sequences. The latest samples of *T.flandrini* are associated with the first attributable to *T.mediterraneum*, though these are fragmentary and difficult to identify with any degree of confidence.

The situation changes in the beds immediately above, with the appearance of easily identifiable *T.mediterraneum* – *T.calliplocum* and few *T.zitteli* forms, together with the first *Metaderoceras* of the *M.evolutum* – *M.gemmellaroi* group. The next association, after the disappearance of *T.mediterraneum* – *T.calliplocum*, is reduced to *T.zitteli* and numerous *Metaderoceras* (*M.evolutum*, *M.gemmellaroi*). At this point, *Dubariceras* (DOMMERGUES et al. 1984) and *Protogrammoceras*, appear for the first time.
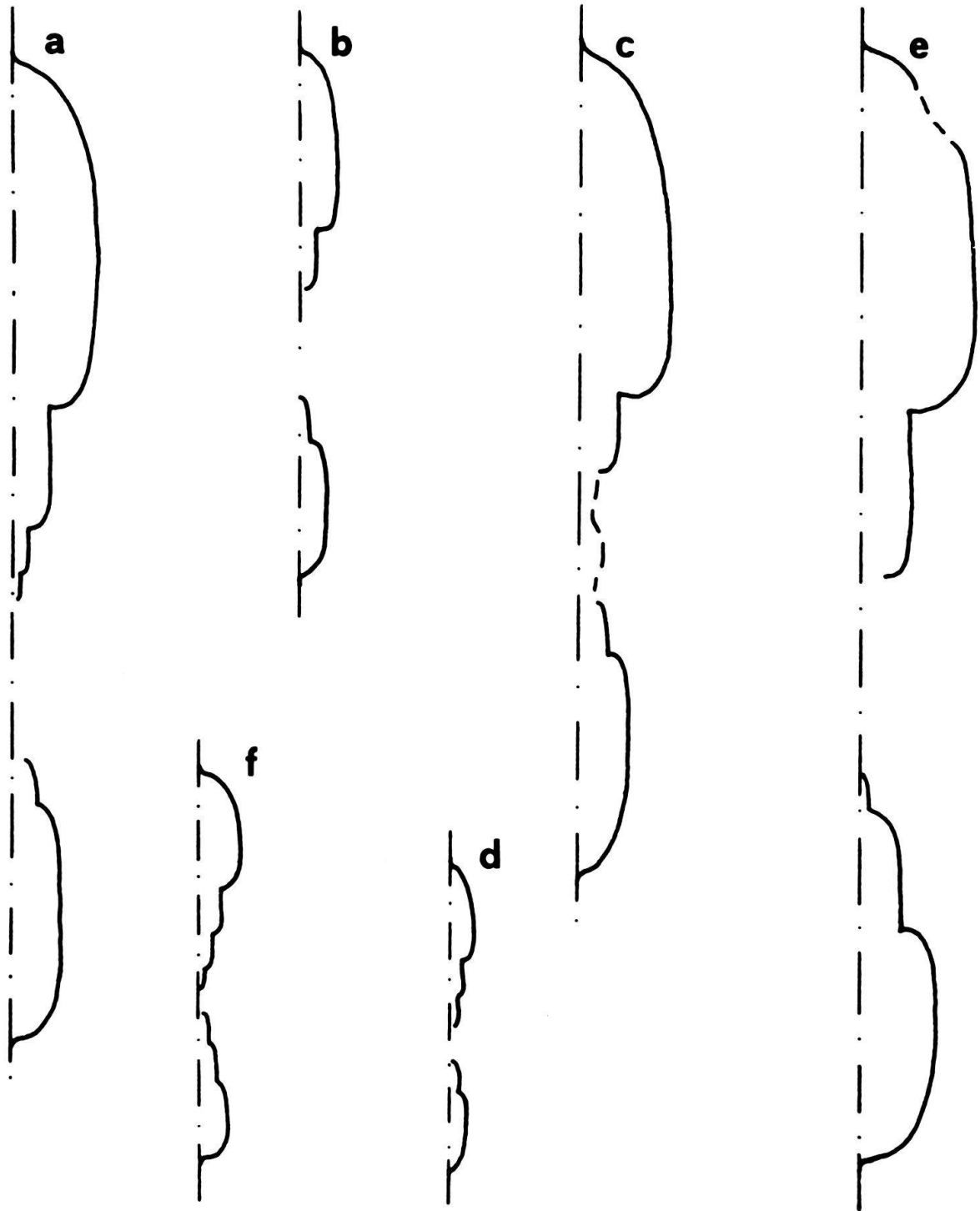
Fig. 9. Whorl-sections of: a) *T. flandrini*, b) *T. demonense*, c) *T. mediterraneum*, d) *T. calliplocum*, e) *T. zitteli* macroconch, f) *T. zitteli* microconch.

The next ammonite association is markedly different, being composed principally of *Dubariceras, Reynesocoeloceras, Radstockiceras, Becheiceras, Protogrammoceras, Fuciniceras* and abundance of Phylloceratina and Lytoceratina.

The Lower, Middle and Upper Carixian of the Subbetic Zone have been defined on the basis of successive associations of *Gemmellaroceras, Tropidoceras – Metaderoceras* and *Reynesocoeloceras – Radstockiceras* (RIVAS 1979), although it is difficult to correlate these chronostratigraphic divisions with those of other regions (Fig. 2).

The correlation of this biochronological scheme with those established in other european areas, such as the type locality Pliensbach (GEYER 1964; SCHLATTER 1977, 1980) and Western Europe (France, England, Portugal, etc.) (DOMMERGUES 1984), is imprecise. Since other significant biostratigraphic indicators are lacking, *Tropidoceras* must serve.

T. flandrini has been found associated with *Uptonia lata* in the Alps (DOMMERGUES 1984). MOUTERDE & TURIN (1984) at Serre-Ponçon found *T. flandrini* (s.l.) slightly below *Uptonia lata*. These occurences place the first record of *T. flandrini* in the Jamesoni Zone (Jamesoni Subzone). Probably our Flandrini horizon can be correlated with the first appearance of *T. flandrini* in Europe. There are, nevertheless, forms imprecisely attributed to *T. flandrini*, or to subspecies (i.e. *T. flandrini obtusa*, SCHLATTER 1980, and *T. flandrini* group, DOMMERGUES 1984) recorded in the Masseanum Subzone. There after the correlation of the Flandrini horizon of the Subbetic Zone to a precise horizon, or even to a given subzone of the North european biochronological divisions is not possible.

T. mediterraneum and *T. calliplocum* have not been recorded outside the Mediterranean area. *T. stahli* has been found associated to *A. arietiforme* and placed in the lower part of the Valdani Subzone (SCHLATTER 1980) or in the Arietiforme horizon of the Masseanum Subzone (DOMMERGUES 1984).

We have obtained the first *T. zitteli* inmediatly after the last record of *T. flandrini*, associated with *T. mediterraneum* and *T. calliplocum*, but *T. zitteli* only becomes frequent in upper strata associated with *Metaderoceras evolutum* and *M. gemmellaroi* when *T. mediterraneum – T. calliplocum* dissapears.

At present a completer or even partial correlation between the appearance of *T. stahli* in north western Europe with that of *T. zitteli* in the Mediterranean, is not possible but, if as we think *T. zitteli* and *T. stahli* are variations of the same biospecies, then a certain correlation between them could be made.

Dimorphism

In the better developed sequences, in which *Tropidoceras* occurs at various levels, we may observe the following morphological sequence of pairs (using the "specific" nomenclature applied above):

1. *T. erythraeum* morphology,
2. *T. demonense–T. flandrini*,
3. *T. calliplocum–T. mediterraneum*,
4. *T. zitteli* (previously occuring, with its own characteristic dimorphism).

In each pair, the juvenile stages are morphologically very similar. The growth of the parameters considered (O, H, E) during ontogeny in either member of each pair coincides with that of the other. The ornamentation, too, is so similar as to make juvenile or
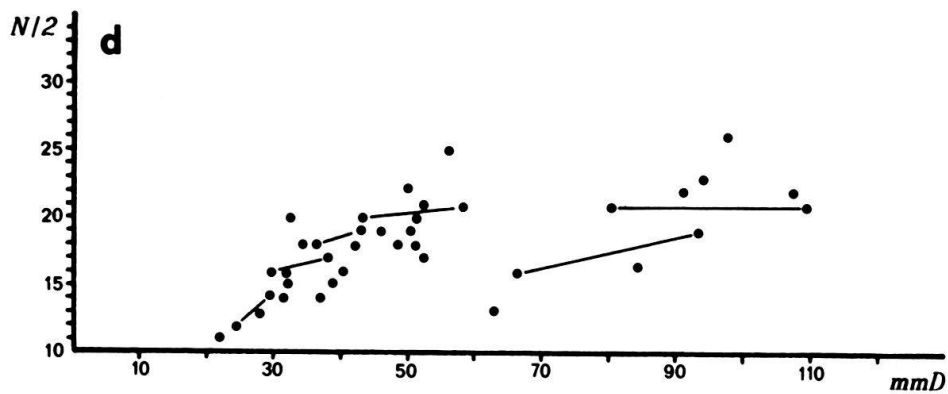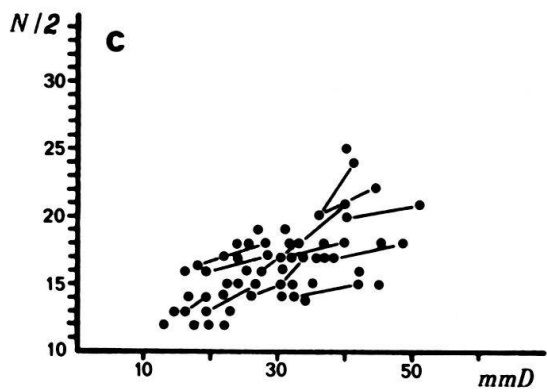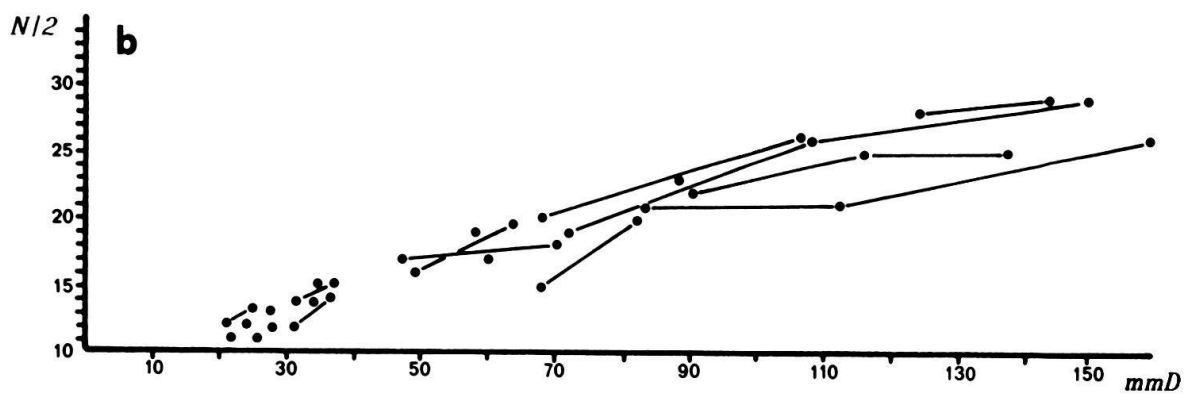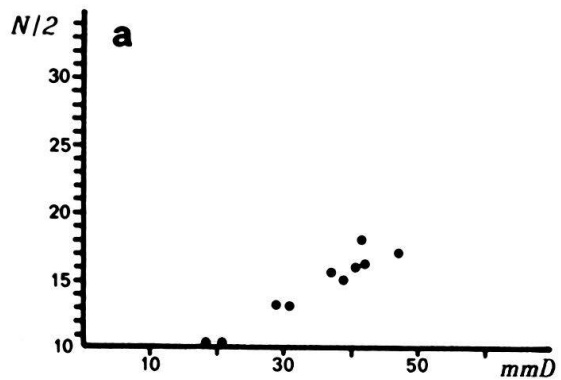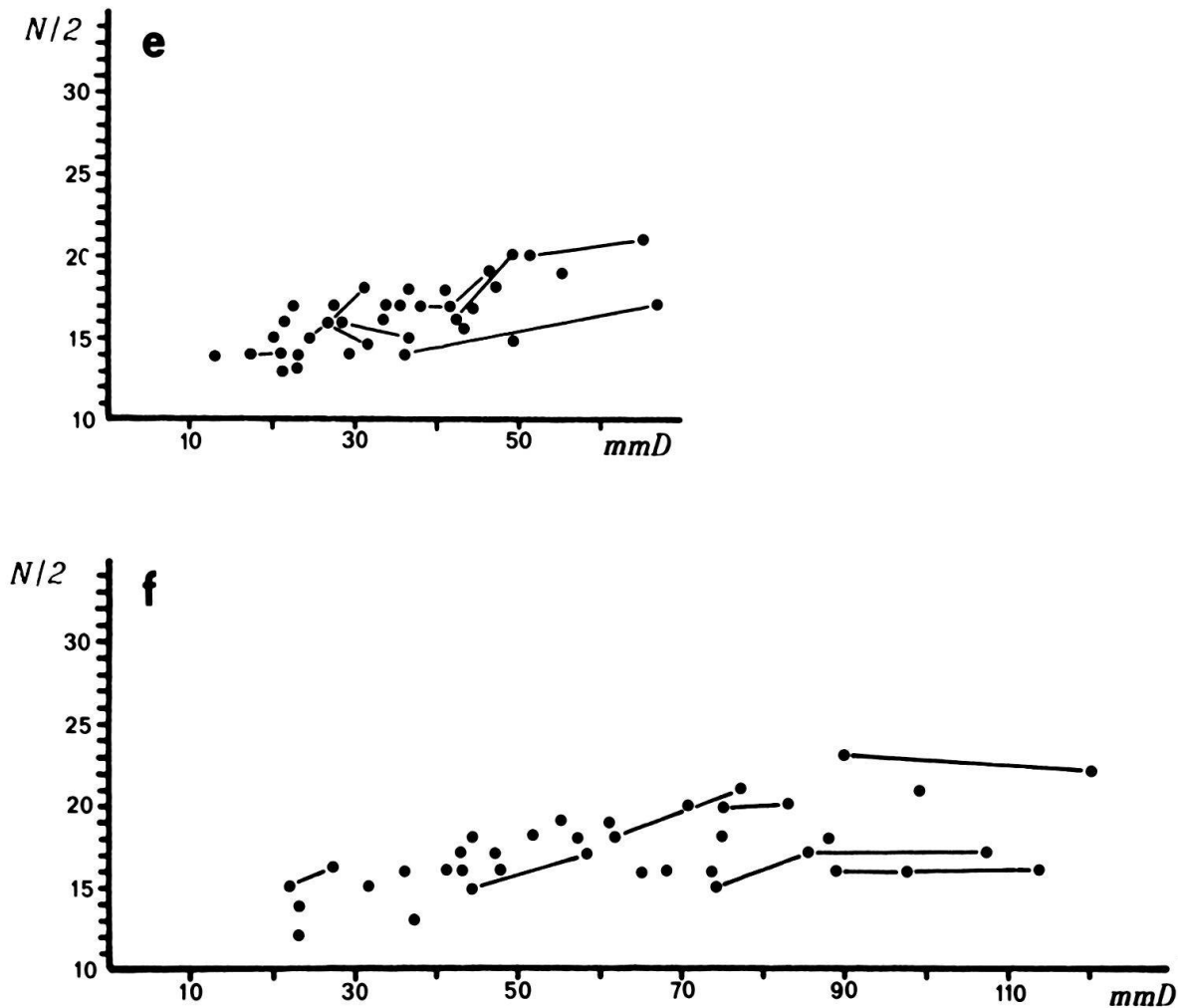
Fig. 10. Ribbing frequency diagrams (D-N/2). a) *T. demonense*, b) *T. flandrini*, c) *T. calliplocum*, d) *T. mediterraneum*, e) *T. zitteli* Macroconch, f) *T. zitteli* Microconch. Note the coincidence of the ribbing frequency fields of both macroconches and corresponding microconches at same size.

fragmentary forms practically indistinguishable. The range of variation in the number of ribs at a given diameter is practically identical in both members of a pair (Fig. 10).

The suture lines at the same diameter are also analogous, not only in their elements and configuration, but also in complexity (Fig. 11). Morphological differences within each pair begin to appear at the end of the preadult stages. While whorl expansion increases with a greater degree of involution in the large forms it remains constant or may actually decrease in the smaller. In the large forms the suture lines become more complex as the whorl height increases.

The ratio of diameters taken at the end of the phragmocone in adult forms is approximately 3/1 in *T. flandrini–T. demonense* (2.7/1) and 4/1 in *T. mediterraneum–T. calliplocum* (3.8/1).

Two morphological groups are distinguishable in *T. zitteli*, large and small forms occuring throughout the biostratigraphic range of the species, despite the scarcity of specimens of the early stages. As in the species already described, the juvenile forms of either group ar indistinguishable by shell shape and ornamentation. The sutures too, are very similar. The size ratio between large and small forms, measured as before, is 3/1.

Fig. 11. External suture lines of: a) *T.erythraeum*, b) *T.flandrini*, c) *T.demonense*, d) *T.mediterraneum*, e) *T.calliplocum*, f) *T.zitteli*. Showing the similarity of the suture patterns within the dimorphic pairs.

The most typical secondary features of ammonite dimorphism are absent in *Tropido-ceras,* but the morphological characteristics already described, together with their vertical distribution suggest intraspecific sexual dimorphism.

This interpretation would lead us to expect a dismorphism in exclusively Northern European *Tropidoceras* (not found in the Mediterranean Realm). The morphologies described as *T. ellipticum, T. lineatum* and *T. futtereri* appear to correspond to microcon-ches and *T. masseanum, T. masseanum rotunda* and *T. flandrini obtusa* to macroconches.

Evolution

Although there are references to *Tropidoceras* in the Upper Sinemurian (GÉCZY 1972, 1976, DONOVAN 1958, PARONA 1896), this chronostratigraphical position of the genus has never been confirmed. GÉCZY places a *Tropidoceras* aff. *actaeon* in the Raricostatum Zone of the Lokut profile, associated with Phylloceratina and Lytoceratina without any biostratigraphical significance. Above this association, there is another, which he places in the Jamesoni Zone, since it contains *Metoxynoticeras* cf. *involutum, Uptonia angusta, Tropidoceras* sp. and *Metaderoceras,* but the difficulty in identification of the Oxynotic-eratidae and the extended temporal distribution of *Metoxynoticeras (Radstockiceras?)* makes this form unsatisfactory as a biostratigraphical index. Furthermore, *Uptonia angusta* really belongs to the new genus *Dubariceras* (cf. DOMMERGUES et al. 1984), which occurs in the Middle Carixian, as do the forms of *Metaderoceras* of the *evolutum-gemmellaroi* group. Therefore, it is more likely that this association belongs to the Ibex Zone (Middle Carixian) and not to the Jamesoni Zone, which would put the *Tropidoceras* aff. *actaeon* attributed to the Raricostatum Zone in an indeterminate position between the Sinemurian s.s. and the Middle Carixian.

DONOVAN (1958) mentions *Tropidoceras* aff. *actaeon* juxtaposed to an Upper Sinemu-rian association in Langeneckgrat. This specimen illustrated by HUG (1899) belongs to the OOSTER Collection in the Natural History Museum in Berne. Nevertheless, DONOVAN himself admits that: "it is perhaps more probable that the specimen really comes from a higher horizon than the fossil bed at Langeneckgrat".

PARONA (1896) described *Cycloceras actaeon* in his monograph on the Lower Liassic of Saltrio, but recognized the possibility that it does, in fact, belong to the Pliensbachian.

The first reliable references to the genus with relevant biochronological associations indicate the upper part of the Lower Carixian. In the western mediterranean region, *Tropidoceras* occurs above "the Lower Carixian forms" and is generally only accom-panied by *Metaderoceras,* so that it is difficult to pinpoint its chronostratigraphic posi-tion (even though its earliest and simplest forms, mentioned above, *(T. erythraeum)* occur with or just above *Gemmellaroceras* and *Coeloceras). T. flandrini* has also been found associated with *Uptonia* (cf. DOMMERGUES 1984, MOUTERDE & TURIN 1984).

SCHINDEWOLF (1962) considers that the Acanthopleuroceratinae derive from Poly-morphitinae. TINTANT & MOUTERDE (1981) derive them from Eoderoceratidae without going into detail, as an independent line of Polymorphitinae, considering them to be "very original forms". SPATH (1928) thought the genus *Tropidoceras* was related to the Polymorphitinae by way of *Polymorphites* or *Gemmellaroceras.* WIEDENMAYER (1980) considered *Bouhanmidoceras* (DUBAR 1962), a genus from the Oxynotum Zone of the High Atlas of Morocco, to be the ancestor of *Tropidoceras.* His argument, however,
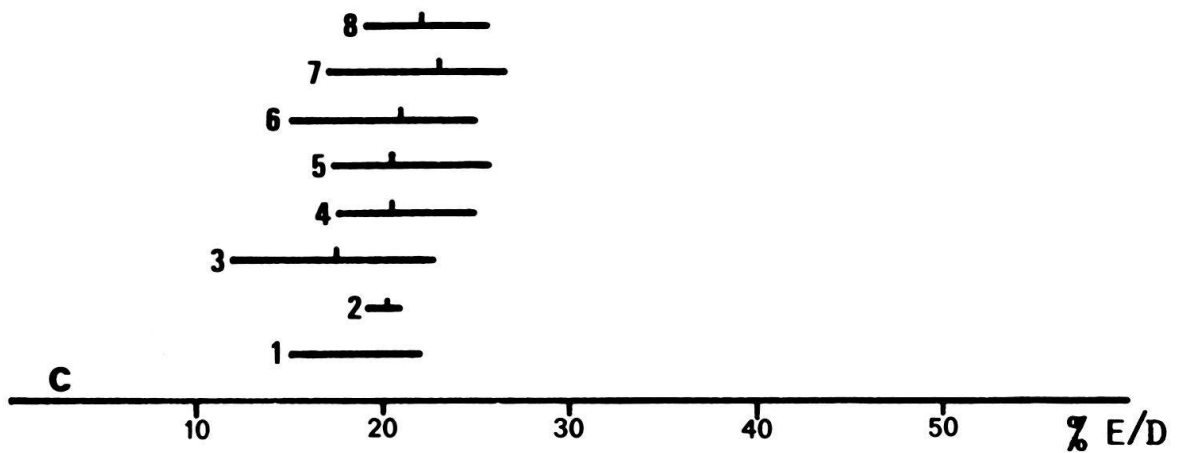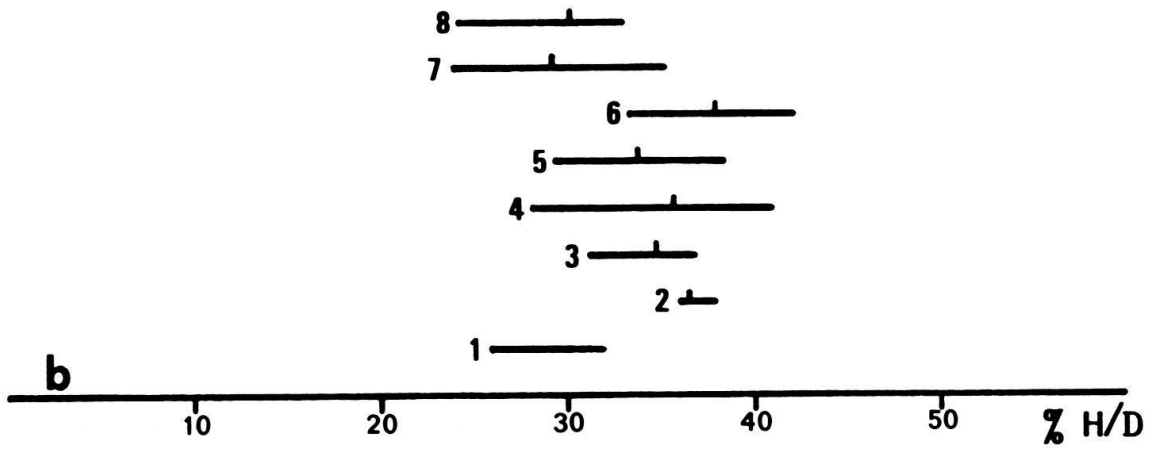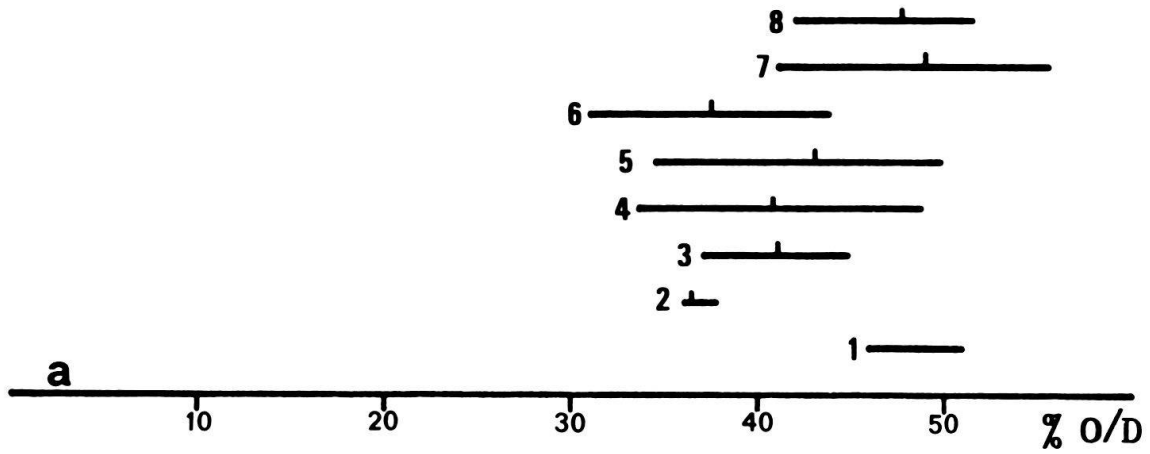
Fig. 12. Ranges and median values of the ratios O/D, H/D and E/D in *Gemmellaroceras* (values taken from GEMMELLARO's figures) and in the studied species (values obtained from our samples). 1. *Gemmellaroceras.* – 2. *T. erythraeum.* – 3. *T. demonense.* – 4. *T. flandrini.* – 5. *T. calliplocum.* – 6. *T. mediterraneum.* – 7. *T. zitteli* Microconch. – 8. *T. zitteli* Macroconch.
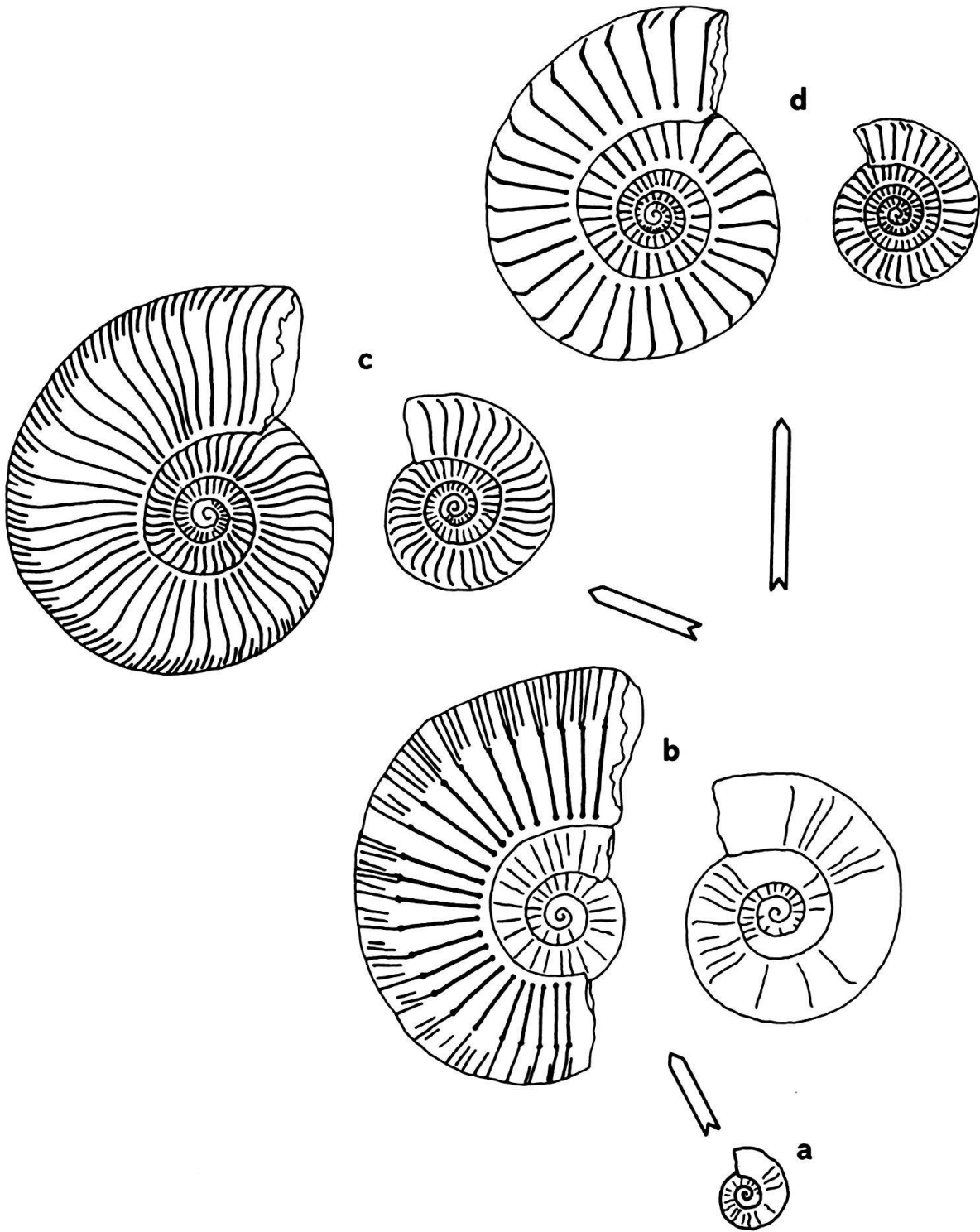
Fig. 13. Evolution and dimorphism of the Mediterranean species of *Tropidoceras*. a) *T. erythraeum*. – b) *T. demonense–T. flandrini*. – c) *T. calliplocum–T. mediterraneum*. – d) *T. zitteli* (microconch-macroconch).

which is based on the similarities of the suture lines, in particular the tendency towards a suspensive lobe in *Bouhanmidoceras*, appears to be far-fetched. There is a major temporal hiatus between the Moroccan genus and the first appearance of *Tropidoceras* (probably in the Jamesoni Zone, discussed above).

Both the stratigraphical position and the morphology of *Gemmellaroceras* are very close to those of the earliest *Tropidoceras*. This is especially true for the forms which have a rudimentary keel (e.g. *G. alloplocum* (GEMMELLARO), Pl. 4, Fig. 17–19), foreshadowing the characteristics of *Tropidoceras*.

It must be also admitted, as SCHINDEWOLF has pointed out, that the suture of the Acanthopleuroceratinae and Polymorphitinae are closely related. The general characteristics of the sutures of *Gemmellaroceras* and the earliest *Tropidoceras* are very similar and they differ only in detail, especially when compared at the same diameter. They share a common development of the external saddle and the lateral and U_2 lobes. The lateral lobe in *Gemmellaroceras* may be bifid or trifid, just like that of juvenile *T. demonense* forms. The relative size of U_2 lobe, with respect the lateral one however, is nonetheless, similar to that of the earliest juvenile *Tropidoceras*. The most obvious distinguishing characteristic lies in the differing of the two parts of the external saddle; in *Gemmellaroceras*, unlike *Tropidoceras*, the internal part is smaller than the external.

The earliest forms of *Tropidoceras*, in our experience, are small and their morphology is not well differentiated; they are almost smooth with irregular incipient ribs *(T. erythraeum)*. In the second stage, corresponding to the expansion of the genus, various other morphologies appear (see the faunal sequence above). These include smooth forms similar to the earliest species, but bigger, together with forms with well developed ornamentation, straight intercalated ribs and small peri-umbilical and ventrolateral tubercles.

The third stage marks a further morphological diversification. Included are forms with characteristics analogous to those of the ancestral species pair, with similar ribbing in large forms *(T. mediterraneum)*, although the ribs are sinuous and lack tubercles. The contemporaneous small forms *(T. calliplocum)*, however, have stronger and denser ribbing than their predecessors. This stage also saw the appearance of quite different forms *(T. zitteli)*, which are subrectangular to subquadrate in section with slower whorl expansion. These have the straight ribbing of *T. flandrini*, although the intercalatory ribs are less frequent. *T. zitteli* survived after the disappearance of *T. mediterraneum* and *T. calliplocum*.

The sutures also present a morphological sequence from initial simple, *Gemmellaroceras*-like structures in *T. erythraeum*, to very complex morphologies, although the number of elements remains constant in *T. flandrini*. Subsequently, they tend to become simple again, with two clearly distinguishable lineages (Fig. 11).

The sutures of the adult specimens belonging to the *T. mediterraneum–T. calliplocum* group closely resemble those juveniles from the preceding *T. flandrini–T. demonense* group, whereas in *T. zitteli* the L lobe becames simplified, tending to trifurcation unlike the other species, which tend to be bifid.

The phylogenetic interpretation of this morphological sequence seems to be clear. The earliest forms of the *T. erythraeum* morphology give rise to *T. flandrini–T. demonense*, and these, in turn, to *T. mediterraneum–T. calliplocum* on the one hand and *T. zitteli*, on the other.

The transition from *Gemmellaroceras* to the primitive *Tropidoceras* implies an acceleration of the *"Gemmellaroceras* character" (venter without keel) in the early stages and then a deviation with acquisition of well developed ornamentation and keel. The evolution of the early *Tropidoceras* into *T. flandrini* and *T. demonense* implies a double process. On the one hand, the supposed microconch *T. demonense* preserved the ornamentation of the preceding species without any important change, but on the other, its suture line became complex.

The ontogeny of the macroconch *T. flandrini* includes a further stage, involving changes in shell shape and ornamentation by the acquisition of new elements such as well-defined ribbing and tubercles. The secondary ribbing, characteristics of *Tropidoceras,* is already clearly defined in this species. The suture line increases in complexity in correlation with whorl height.

These forms give rise to two well-defined morphological groups: the pair *T. mediterraneum–T. calliplocum* and *T. zitteli.*

The pair *T. mediterraneum–T. calliplocum* (macro and microconches) preserve the general patterns. The suture, although still complex, is clearly paedomorphic in its resemblance to the early stages of *T. flandrini–T. demonense.* The ornamentation becomes simpler, more sinousous, lacking tubercles.

In the Subbetic Zone the transition from *T. flandrini–T. demonense* to *T. zitteli* is marked by an apparently abrupt change in ornamentation and shell development.

Some individuals of *T. flandrini,* nevertheless, exhibit in the phragmocene characteristics foreshadowing those of *T. zitteli.* Finally, the evoultion of this last species can be explained by an ontogenetic retardation in the development of the secondary and intercalatory ribbing, characteristic of the adult stages of *T. flandrini.*

Paleobiogeographical Distribution

The birth-place of *Tropidoceras* is difficult to establish; the earliest forms (with ill-defined characters) are found both in the Mediterranean Realm and in the Boreal-subboreal region.

Furthermore, *Gemmellaroceras,* the supposed ancestor of the genus is found in both biogeographical areas in the Lower Carixian, though more abundantly and persistently in the Mediterranean Realm.

Although early *Tropidoceras* have only been studied in relatively few sites in the Mediterranean region, they seem to be more abundant than in North Western Europe.

References to *T. flandrini* (s.str.) in the Boreal-subboreal region are scacre, leading us to suppose that they originated in the Western Mediterranean, where they abound and spread sporadically to the North. This species is also represented in that region by *T. flandrini* var. *obtusa* and *T. flandrini densicosta* whose coexists with, and even persists after, *T. stahli* (SCHLATTER 1980). *T. demonense* has a similar biogeographic pattern; it is very frequent in the Subbetic Zone, but very rare in the northwestern european realms [i.e. MEISTER 1984, found it in France (Causses), Pl. 8, Fig. 2].

T. mediterraneum and *T. calliplocum* are confined to the Mediterranean. Their northern morphological equivalent is *T. masseanum,* which probably antedates them, since it never coexists with the first *T. stahli.* If the hypothesis of DOMERGUES & MOUTERDE (1978) is correct, *T. masseanum* is derived from the earliest Tethyan emigrants in the European

basins. MEISTER (1984) cites *T. calliplocum* in the Causses (France) but the figured exemplar is atypical, largely different from those of the Mediterranean Realm.

According to DOMMERGUES & MOUTERDE (1978), a descendeant of *T. masseanum* (*Tropidoceras* sp. of these authors) subsequently gave rise to typical *Acanthopleuroceras*, which barely reached the Tethys and have not been found in the Western Mediterranean.

Although *T. zitteli* do not occur in North West Europe, *T. stahli*, as we have seen, may be a geographical variation.

HILLEBRANDT (1979) mentions *Tropidoceras* gr. *stahli* and *T.* sp. gr. *flandrini* in the Lower Pliensbachian of Atuel River (Mendoza Province, Argentina) and fragmentary remains in Chile and Peru. These *Tropidoceras* are found below "*Uptonia*", which probably corresponds to *Dubariceras*. *M. evolutum* have been found associated with *Tropidoceras* in Peru and constitute the only correlation index with our sequences. Unfortunately *M. evolutum* is associated to unidentified *Tropidoceras* and precise correlation with european forms still is difficult.

In British Columbia and Alaska, FREBOLD (1970) and IMLAY (1981) also cite *Tropidoceras* (*T.* sp. and *T. actaeon*), morphologically close to *T. calliplocum*, having a biostratigraphic position similar to those of the Subbetic Zone. The presence of *Tropidoceras* with Mediterranean affinities supports the hypothesis of the existence of an "Atlantic seaway" during Carixian times.

Acknowledgments

Table 1 — Index values:

Species	O/D n	O/D vM	O/D vm	O/D x̄	O/D s	H/D n	H/D vM	H/D vm	H/D x̄	H/D s	E/D n	E/D vM	E/D vm	E/D x̄	E/D s	N/2 n	N/2 vM	N/2 vm	N/2 x̄	N/2 s
T. erythraeum	4	0'38	0'36	0'36	0'008	4	0'38	0'36	0'37	0'008	4	0'21	0'19	0'20	0'008	-	--	--	--	-
T. flandrini	79	0'49	0'34	0'41	0'03	79	0'41	0'28	0'36	0'02	40	0'25	0'18	0'21	0'02	34	29	11	18	5'63
T. demonense	21	0'45	0'37	0'41	0'02	21	0'37	0'31	0'35	0'02	9	0'23	0'14	0'18	0'03	9	18	10	14	2'74
T. mediterraneum	58	0'45	0'31	0'38	0'03	18	0'42	0'33	0'38	0'02	36	0'25	0'15	0'21	0'02	37	26	13	18	4'02
T. calliplocum	108	0'50	0'34	0'43	0'03	108	0'38	0'29	0'34	0'02	32	0'26	0'17	0'21	0'02	75	25	10	16	2'75
T. zitteli (macro)	55	0'52	0'42	0'48	0'02	55	0'33	0'24	0'30	0'02	24	0'26	0'19	0'22	0'01	36	23	12	17	2'40
T. zitteli (micro)	50	0'56	0'41	0'49	0'04	49	0'35	0'24	0'29	0'03	28	0'27	0'17	0'23	0'02	37	21	13	16	2'03

Regression equations and correlations:

T. flandrini
- D-O: $y=0'56x^{0'92}$ cc=0'99; $y=1'87+0'37x$ cc=0'99
- D-H: $y=0'28x^{1'06}$ cc=0'99; $y=-0'72+0'37x$ cc=0'99
- D-E: $y=0'22x^{0'98}$ cc=0'99; $y=0'23+0'20x$ cc=0'98

T. demonense
- D-O: $y=0'38x^{1'02}$ cc=0'99; $y=0'02+0'41x$ cc=0'99
- D-H: $y=0'37x^{0'99}$ cc=0'99; $y=0'23+0'34x$ cc=0'99
- D-E: $y=0'87x^{0'58}$ cc=0'86; $y=0'350+0'1x$ cc=0'84

T. mediterraneum
- D-O: $y=0'49x^{0'93}$ cc=0'99; $y=1'05+0'35x$ cc=0'99
- D-H: $y=0'33x^{1'03}$ cc=0'99; $y=0'16+0'38x$ cc=0'99
- D-E: $y=0'22x^{0'98}$ cc=0'97; $y=-0'03+0'21x$ cc=0'97

T. calliplocum
- D-O: $y=0'45x^{0'99}$ cc=0'97; $y=0'48+0'43x$ cc=0'97
- D-H: $y=0'41x^{0'94}$ cc=0'97; $y=0'62+0'32x$ cc=0'97
- D-E: $y=0'31x^{0'88}$ cc=0'95; $y=0'75+0'18x$ cc=0'94

T. zitteli (macro)
- D-O: $y=0'49x^{0'99}$ cc=0'99; $y=1'29+0'46x$ cc=0'99
- D-H: $y=0'30x^{1'01}$ cc=0'98; $y=0'56+0'32x$ cc=0'98
- D-E: $y=0'28x^{0'94}$ cc=0'98; $y=1'04+0'21x$ cc=0'98

T. zitteli (micro)
- D-O: $y=0'48x^{1'01}$ cc=0'98; $y=0'64+0'51x$ cc=0'98
- D-H: $y=0'32x^{0'98}$ cc=0'97; $y=0'72+0'27x$ cc=0'97
- D-E: $y=0'57x^{0'74}$ cc=0'94; $y=2'57+0'15x$ cc=0'93

Table 1. Indexes and correlations of the whorl parameters. D: diameter; O: umbilical diameter; H: whorl height; E: whorl width; N/2: number of ribs per half whorl.

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Plate 1

Fig. 1   *T. erythraeum* (GEMMELLARO). – CP4i-16. Cortijo Pilas (Jaén). Lower-Middle Carixian bound-
         ary. Small adult (?) example with rostrum.

Fig. 2   *T. erythraeum* (GEMMELLARO). – CP4s-4. Cortijo Pilas (Jaén). Middle Carixian. Small fragmen-
         tary example with rostrum partially conserved.

Fig. 3   *T. flandrini* (DUMORTIER): – CP4s-1. Cortijo Pilas (Jaén). Middle Carixian. Small phragmocne.
         It is possible to observe how close this morphology is to that of *T. demonense* (see Fig. 3 and 5).

Fig. 4   *T. demonense* (GEMMELLARO). – CP4s-46. Cortijo Pilas (Jaén). Middle Carixian. Slightly de-
         formed phragmocone.

Fig. 5   *T. demonense* (GEMMELLARO). – CP4s-27. Cortijo Pilas (Jaén). Middle Carixian. Slightly defor-
         med adult example with body chamber.

Fig. 6   *T. demonense* (GEMMELLARO). – CP4s-25. Cortijo Pilas (Jaén). Middle Carixian. Adult example
         with body chamber.

Plate 2

Fig. 1   *T. flandrini* (DUMORTIER). – CP4s-24. Cortijo Pilas (Jaén). Middle Carixian. Phragmocone with poorly developed upper row of tubercles.

Fig. 2   *T. calliplocum* (GEMMELLARO). – CO2.1.51. Cortijo Puerto Ortiz (Murcia). Middle Carixian. Phragmocone.

Fig. 3   *T. calliplocum* (GEMMELLARO). – MZ6.5.1. Cortijo Majarazan (Murcia). Middle Carixian. Phragmocone.

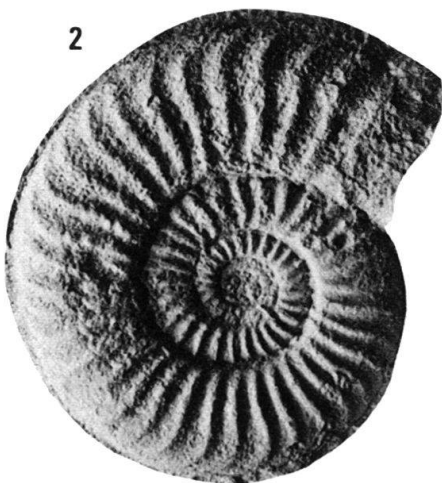Fig. 4   *T. calliplocum* (GEMMELLARO). – MZ5.-3.13. Cortijo Majarazan (Murcia). Middle Carixian. Phragmocone.

Plate 3

Fig. 1   *T. mediterraneum* (GEMMELLARO). – G.1.1. Garrumbre (Murcia). Middle Carixian. Inmature example with body chamber.

Fig. 2   *T. calliplocum* (GEMMELLARO). – MZ5.-3.51. Cortijo Majarazan (Murcia). Middle Carixian. Phragmocone.

Fig. 3   *T. calliplocum* (GEMMELLARO). – CA.015.1. Cueva del Agua (Granada). Middle Carixian. Phragmocone.

Fig. 4   *T. mediterraneum* (GEMMELLARO). – MZ5.-3.47. Cortijo Majarazan (Murcia). Middle Carixian. Outer whorls of phragmocone.

Fig. 5   *T. zitteli* FUCINI. Microconch. – CO2.3.2. Cortijo Puerto Ortiz (Murcia). Middle Carixian. Adult example with the body chamber partially preserved.

Fig. 6   *T. zitteli* FUCINI. Microconch. – BAO.1 (auxiliary sequence in Cueva del Agua area (Granada)). Middle Carixian. Almost complete inmature example.

Fig. 7   *T. mediterraneum* (GEMMELLARO). – MZ5.-3.42. Cortijo Majarazan (Murcia). Middle Carixian. Inner whorls in which the similarity to *T. calliplocum* is clearly observed.
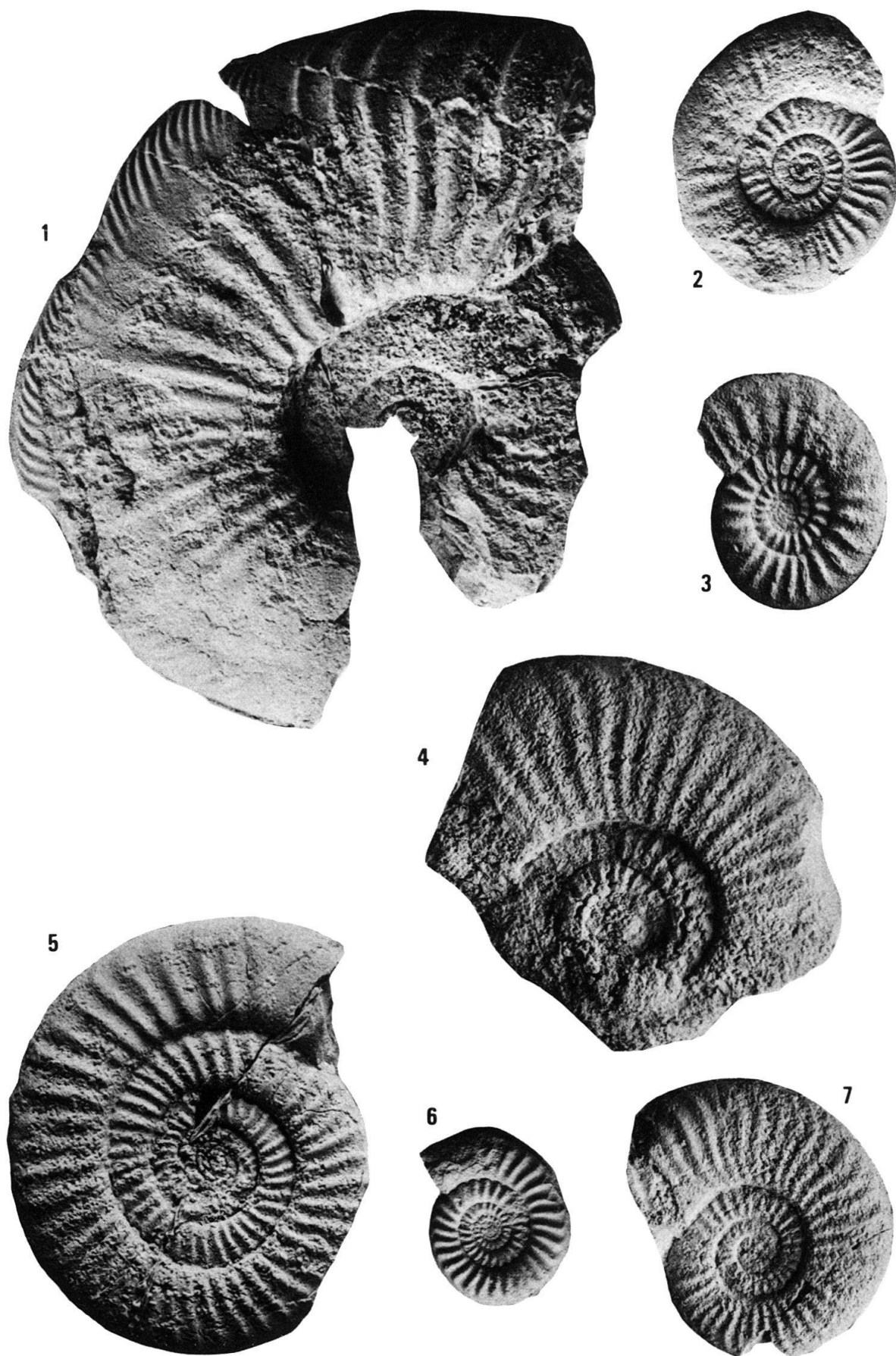
Plate 4

Fig. 1   *T. zitteli* FUCINI. Macroconch. – CO2.3.10. Cortijo Puerto Ortiz (Murcia). Middle Carrixian. Phragmocone.

Fig. 2   *T. zitteli* FUCINI. Microconch. – CP2.3.2. Cortijo Pilas (Jaén). Middle Carixian. Phragmocone and body chamber of a small example.

Fig. 3   *T. zitteli* FUCINI. Macroconch. – CO2.3.21. Cortijo Puerto Ortiz (Murcia). Middle Carrixian. Phragmocone showing the most sinuous ribbing observed in our sample.

Fig. 4   *T. zitteli* FUCINI. Macroconch. – CO2.3.3. Cortijo Puerto Ortiz (Murcia). Middle Carrixian. Phragmocone.

Fig. 5   *T. zitteli* FUCINI. Microconch. – CO2.3.15. Cortijo Puerto Ortiz (Murcia). Middle Carrixian. Phragmocone.