# Upper Toarcian – Middle Aalenian (Jurassic) Erycitinae SPATH (Ammonitina) from the Gerecse Mts, Hungary

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(with 12 figures, 4 tables and 13 plates)

The Upper Toarcian–Middle Aalenian sequences of the Gerecse Mts belong to the Mediterranean region of the Mediterran–Caucasian Realm, bigger part of the Ammonoidea collected here are represented by the suborders Phylloceratina and Lytoceratina. In this paper the species belonging to the subfamily Erycitinae SPATH are documented as a contribution to the general taxonomic and biostratigraphic revision of the Ammonitina fauna. Considering the abundance and diversity of the subfamily, it was a dominant group in the Meneghinii to Opalinum Zones: during its acme Erycitinae formed 52% of the Ammonitina. Two genera, one subgenus and 15 species are represented by 117 determined specimens. Quantitative evaluation and problems of systematics are briefly discussed, genera and species are described. Introduction of two new taxa, *Cagliceras enigmaticum* n. sp. and *Erycites gerecsensis* n. sp. is designated.

Key words: Ammonitina, Erycitinae, *Cagliceras*, *Erycites*, Abbasitoides, Jurassic, Toarcian, Aalenian, Gerecse Mts, Hungary

### Introduction

The present study is a contribution to the documentation and biostratigraphic and paleobiogeographic investigation of the Toarcian and Aalenian Ammonitina fauna of the Gerecse Mts. An extensive collecting work was carried out in five sections of the Gerecse Mts (Figure 1) between 1976-1982, by the staff of the Geological Institute of Hungary. (There are two sections at the Tölgyhát Quarry: "A" and "B".) The first quantitative, taxonomic and paleobiogeographic analyses of the Ammonoidea material were published by GÉCZY (1984, 1985a, 1985b, 1990). Based on the latest results, GÉCZY &

SZENTE (2007) completed a detailed revision of the Middle Toarcian (Bifrons and Gradata Zones) Ammonitina fauna, and discussed its paleobiogeographic consequences. The aim of this paper is to provide quantitative and biostratigraphic evaluation as well as taxonomic documentation of specimens belonging to the Upper Toarcian – Middle Aalenian subfamily Erycitinae SPATH. The material is deposited in the Natural History Museum of the Faculty of Sciences of Eötvös Loránd University, Budapest.

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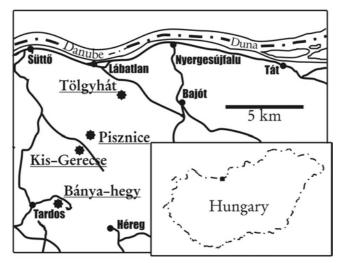


Figure 1. Toarcian – Aalenian sections in the Gerecse Mts.

# Stratigraphy

# Lithostratigraphy

A detailed lithological analysis of the Jurassic sequences of the Gerecse Mts was carried out by CSÁSZÁR et al. (1998). Accordingly, the Toarcian and Aalenian stages are characterised by the "Ammonitico Rosso marl" facies, which developed in two subfacies. The Kisgerecse Marl Formation is typical of the Toarcian (Tenuicostatum to Meneghinii Zones). It is thin-bedded, red nodular marl with variable carbonate and clay content. The Tölgyhát Limestone Formation appears in the Upper Toarcian, is dominating in the Aalenian, and it can be traced to the Humphresianum Zone of the Bajocian. This subfacies is a well-bedded, red, hard nodular limestone. Both lithostratigraphic units are rich in ammonoid assemblages, however the Upper Toarcian - Aalenian fauna mainly consists of poorly preserved inner casts.

# Biostratig raphy

On the ground of the frequent and well-preserved ammonites, it was possible to demonstrate a detailed stratigraphic subdivision (subzones, horizons) in the succession of the Middle Toarcian of the Gerecse Mts (GÉCZY & SZENTE, 2007). As opposed to this, the rarity or lack of the index fossils BUCKMAN, Phlyseogrammoceras Pseudolioceras BUCKMAN, Osperlioceras KRYMHOLZ, Pleydellia BUCKMAN, Leioceras HYATT), as well as the poor state of preservation provide only a limited opportunity for zone- or subzone-level ammonite stratigraphy of the Upper Toarcian (GÉCZY, 1984:383) and the Middle Aalenian. However, one of the most important upshots of the first examinations was that the Upper Toarcian biostratigraphic subdivision of the Northwest European region can be applied to an Ammonitina fauna representing the Mediterranean region. Detailed correlations of the two regions were discussed by GÉCZY (1984, 1985a, 1990). Recent work has resulted in the taxonomic and stratigraphic revision of the Upper Toarcian – Middle Aalenian ammonite assemblages. Consequently, it seems evident, that the biozones proposed by ELMI et al. (1997), CONTINI et al. (1997) and PAGE (2003) are acceptable for the subdivision of sections in the Gerecse Mts as well (Tables 1-4).

# Upper Toarcian biozones

Thouarsense Zone

The base of this zone coincides with the first appearance of *Grammoceras thouarsense* (D'ORBIGNY) or *Pseudogrammoceras bingmanni* (DENCKMANN). The zone can be demonstrated from 4 sections (Pisznice, Kis-Gerecse, Bánya-hegy, Tölgyhát "A") with an average thickness of 120 cm. The fauna consists of Phylloceratina (49%), Lytoceratina (15%), and Ammonitina (36%). The following taxa are described from the Thouarsense Zone:

Polyplectinae: Polyplectus discoides (ZIETEN)

Phymatoceratidae: *Mouterdeiceras masciadrii* (PELOSIO), *M. viticola* ELMI et RULLEAU, *M. escherilobatum* (GÉCZY), *Denckmannia tumefacta* BUCKMAN

Grammoceratinae: Grammoceras thouarsense (D'Orbigny), G. andax Buckman, Pseudogrammoceras subfallaciosum Buckman, P. bingmanni (Denckmann), P. subregale Pinna, P. placidum Buckman, P. pachu Buckman, P. differens (Ernst), P. mediterraneum Gomez et Rivas

Paroniceratinae: *Paroniceras sternale* (BUCH in D'ORBIGNY), *Oxyparoniceras telemachi* (RENZ)

Hammatoceratinae: *Geczyceras bonarellii* (PARISCH et VIALE), *G. porcarellense* (BONARELLI).

#### Speciosum Zone

The zone is defined by the first occurrence of *Pseudolillia emiliana* (REYNÈS). It can be demonstrated from 4 sections (Pisznice, Kis-Gerecse, Bánya-hegy, Tölgyhát "A") with an average thickness of 98 cm. The fauna consists of Phylloceratina (51%), Lytoceratina (21%), and Ammonitina (28%). The following taxa are documented from the Speciosum Zone:

Polyplectinae: *Polyplectus discoides* (ZIETEN) Phymatoceratidae: *Mouterdeiceras* sp.

Grammoceratinae: *Pseudogrammoceras subfalla*ciosum BUCKMAN, *P. cotteswoldia* BUCKMAN, *P.* pedicum BUCKMAN, *P. differens* (ERNST), *Pseudolilia* emiliana (REYNÈS), *P. murvillensis* MAUBEUGE

Hammatoceratinae: Hammatoceras insigne (SCHÜBLER in ZIETEN), H. aff. semilunatum (QUENSTEDT), H. capuccinum BUCKMAN, H. pachu (BUCKMAN), Geczyceras speciosum (JANENSCH), G. bonarellii (PARISCH et VIALE), G. porcarellense (BONARELLI), G. perplanum (PRINZ), Crestaites victorii (BONARELLI), C. meneghinii (BONARELLI), C. goyi (MARTINEZ), C. raricostatus (GÉCZY)

Erycitinae: Cagliceras crassiventris (MERLA), C. picenum (MERLA), C. elaphum (MERLA), C. enigmaticum n. sp.

#### Meneghinii Zone

The base of this zone coincides with the first appearance of species belonging to the genus *Dumortieria* HAUG. The zone can be demonstrated from 4 sections (Pisznice, Kis-Gerecse, Bánya-hegy, Tölgyhát "A") with an average thickness of 100 cm. The fauna consists of Phylloceratina (60%), Lytoceratina (22%), and Ammonitina (18%). The following taxa are described from the Meneghinii Zone:

Dumortieriinae: *Dumortieria meneghinii* (ZITTEL), *D. taramellii* (FUCINI), *D. stricta* PRINZ, *D. evolutissima* PRINZ, *D. evolutissima multicostata* GÉCZY

Hammatoceratinae: Geczyceras perplanum (PRINZ), Crestaites victorii (BONARELLI), Planammatoceras tenuinsigne (VACEK), P. sp. aff.. planinsigne (VACEK), Pseudammatoceras sp.

Erycitinae: Cagliceras elaphum (MERLA), C. crassiventris (MERLA), C. robustum (MERLA), C. rotundiformis (MERLA), Erycites ovatus GÉCZY, Erycites barodiscus GEMMELLARO.

## Aalensis Zone

The base of the zone is defined by the first occurrence of genera *Pleydellia* or *Cotteswoldia* Buckman. The zone can be demonstrated from 3 sections (Pisznice, Kis-Gerecse, Tölgyhát "A") with an average thickness of 101 cm. The fauna consists of

Phylloceratina (73%), Lytoceratina (14%), and Ammonitina (13%). The following taxa represent the Aalensis Zone:

Polyplectinae: Polyplectus discoides (ZIETEN)

Dumortieriinae: Dumortieria meneghinii (ZITTEL), D. stricta PRINZ, Catulloceras dumortieri (THIOLLIÈRE in DUMORTIER), C. pannonica (GÉCZY), Pleydellia laevigata (HANTKEN in PRINZ), Pleydellia sp. aff. particostata BUCKMAN, Cotteswoldia subcompta (BRANCO), Pleydellia sp.

Hammatoceratinae: *Planammatoceras* sp. aff. *planinsigne* (VACEK), *P. tenuinsigne* (VACEK), *Planammatoceras* sp., *Bredyia subinsignis* (OPPEL), *Pseudammatoceras brancoi* (PRINZ)

Erycitinae: Cagliceras elaphum (MERLA), C. rotundiformis (MERLA), C. robustum (MERLA), C. costulosum (MERLA), Erycites ovatus GÉCZY, E. barodiscus GEMMELLARO, E. subquadratus GÉCZY, Erycites gerecsensis n. sp.

#### Aalenian biozones

#### Opalinum Zone

The base of this zone coincides with the first appearance of the genus *Leioceras*. The zone can be demonstrated from 4 sections (Pisznice, Kis-Gerecse, Tölgyhát "A", Tölgyhát "B") with an average thickness of 93 cm. The fauna consists of Phylloceratina (64%), Lytoceratina (14%), and Ammonitina (22%). The following taxa are documented from the Opalinum Zone:

Dumortieriinae: *Tmetoceras* sp., *Catulloceras* sp. Leioceratinae: *Leioceras* sp. aff. *comptum* (REINECKE), *Leioceras* sp.

Hammatoceratinae: *Planammatoceras tenuinsigne* (VACEK), *P. planinsigne* (VACEK), *Bredyia* sp., *Ceccaites sieboldi* (OPPEL), *Csernyeiceras verpillierense* (ROMAN et BOYER), *Planammatoceras* sp., *Pseudammatoceras* sp.

Erycitinae: Cagliceras elaphum (MERLA), C. robustum (MERLA), Erycites fallifax ARKELL, E. ovatus GÉCZY, E. barodiscus GEMMELLARO, E. intermedius HANTKEN in PRINZ, E. subquadratus Géczy, Abbasitoides modestus (VACEK).

# Murchisonae Zone

The zone is indicated by the first occurrence of species belonging to genera *Ancolioceras* BUCKMAN, *Staufenia* POMPECKJ or *Brasilia* BUCKMAN. The zone can be demonstrated from 4 sections (Pisznice, Kis-Gerecse, Tölgyhát "A", Tölgyhát "B") with an average thickness of 112 cm. The fauna consists of Phylloceratina (75%), Lytoceratina (17%), and Ammonitina (8%). The following taxa represent the Murchisonae Zone:

Dumortieriinae: *Tmetoceras scissum* (BENECKE) Leioceratinae: *Staufenia sinon* (BAYLE), *S. noszkyi* (GÉCZY), *Ancolioceras* sp. Graphoceratinae: *Ludwigia murchisonae* (SOWERBY), *L. obtusiformis* (BUCKMAN), *Ludwigia* sp., *Brasilia* sp.

Hammatoceratinae: *Planammatoceras kochi* PRINZ, *Pseudammatoceras spinosum* (HANTKEN in PRINZ), *P. rugatum* (BUCKMAN), *Ceccaites sieboldi* (OPPEL), *C. sieboldi stenomphalum* (PRINZ), *Accardia* sp. aff. *lorteti* (DUMORTIER), *Planammatoceras* sp., *Pseudaptetoceras* sp.

Erycitinae: *Erycites intermedius* HANTKEN in PRINZ, *E. fallifax* ARKELL, *E. ovatus* GÉCZY, *Erycites* sp. aff. *reussi* (HAUER), *Abbasitoides modestus* (VACEK)

Strigoceratinae: *Strigoceras praenuntium* (BUCKMAN)

Oppeliinae: Bradfordia sp.

#### Concavum Zone

It is not possible to demonstrate this zone with certainty. On the basis of its Ammonitina assemblage, the bed 21 of Tölgyhát "B" section belongs to the Murchisonae Zone, whereas bed 18 belongs to the Discites Zone (Cresta & Galácz, 1990:167). However, the material of beds 19-20 (*Phylloceras* sp., *Lytoceras* sp.) does not allow us to prove the presence of the Concavum Zone. Beds 47-49 of the Pisznice section with a fauna consisting of *Graphoceras*? sp., *Pseudaptetoceras* sp., *Phylloceras* sp., *Lytoceras* sp. probably belong to the Concavum Zone, although the exact determination of the zone requires more collecting work.

# A general evaluation of the Ammonitina fauna

The present statistical summary takes notice of the unpublished preliminary reports compiled by GÉCZY forthwith after the collecting work (GÉCZY, 1976, 1977, 1978, 1979, 1980, 1981) as well as the recent revision of the ammonite material.

The pure Mediterranean character of the Toarcian ammonoid fauna of the Gerecse Mts was circumstantially described by GÉCZY (1984, 1985a, 1985b) and GÉCZY & SZENTE (2007). Considering the whole material, Phylloceratina and Lytoceratina form 64% in the Thouarsense Zone, and their ratio reached 92% in the Murchisonae Zone. Furthermore, the Ammonitina assemblage shows a remarkable taxonomic affinity to the Upper Toarcian – Middle Aalenian faunas of Italy and Greece (GÉCZY, 1990).

In the Gerecse Mts the Upper Toarcian – Middle Aalenian Ammonitina are represented by two superfamilies, Hildocerataceae HYATT and Hammatocerataceae SCHINDEWOLF. The family Dactylioceratidae HYATT (superfamily Eoderocerataceae SPATH), which had been persistent during the Early and Middle Toarcian, became extinct at the end of the Clausus Subzone. The majority of taxa present in the Thouarsense Zone (Polyplectinae, Paroniceratinae, Grammoceratinae, Phymatoceratidae) belonged to the Hildocerataceae (88%), although the Hammatocerataceae had started its progressive expansion. The stratigraphically oldest representative of the family Hammatoceratidae, i.e. the genus Rarenodia VENTURI appears in the Bifrons Subzone, then it is the Gradata Zone when the earliest species belonging to the genus Geczyceras [G. costatum (GABILLY) and G. clausum (GABILLY)] turn up. The latter genus represents the subfamily Hammatoceratinae in the Thouarsense Zone as well. A striking evolutionary change occurred in the Speciosum Zone: percentage of Hildoceratidae and

Phymatoceratidae was reduced to 25%, while the ratio of the Hammatoceratinae and Erycitinae increased to 75% (Figure 2). The Speciosum Zone is characterised by the 70% superiority of Hammatoceratinae genera (Geczyceras, Hammatoceras, Crestaites). From the Meneghinii Zone to the uppermost Murchisonae Zone Hammatocerataceae (Hammatoceratinae, the Dumortieriinae, Leioceratinae, Erycitinae, Graphoceratinae) prevails over the fauna. Genus Dumortieria dominates the Meneghinii Zone with 52%, whereas the subfamily Erycitinae shows the same percentage in the Aalensis Zone.

In addition to the ascendancy of genus Leioceras, Hammatoceratinae (Planammatoceras, the Pseudammatoceras, Bredyia, Csernyeiceras) form 32% of the whole fauna in the Opalinum Zone. Considering the Gerecse ammonite assemblage, the genus Csernyeiceras GÉCZY is restricted to this chronozone, its number of specimens (76) constitutes almost half (49%) of the hammatoceratids. The Murchisonae Zone is characterised by the dominance of genera representing subfamilies Leioceratinae and Graphoceratinae (Staufenia, Ancolioceras, Ludwigia, Brasilia) with a proportion 60% on the one hand, and by the regression of Hammatoceratinae on the other. It is the Bradfordensis Subzone when the earliest taxa of the superfamily Haplocerataceae Zittel (Strigoceras praenuntium, Bradfordia sp.) appear. Comparing the Gerecse ammonites with other Aalenian faunas, the remarkably low number of the genus Tmetoceras Buckman in the Gerecse Mts (6 specimens, 1.3%) is worth mentioning. The Erycitinae can be first documented from the Speciosum Zone. They became diverse and abundant from the Meneghinii Zone, dominate the Aalensis Zone, then show a decline in the Murchisonae Zone and finally disappear from the assemblage (Figure 3).

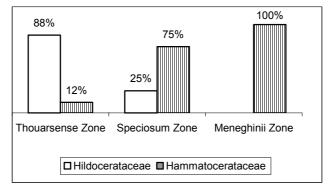


Figure 2. Ratio of superfamilies Hildocerataceae and Hammatocerataceae in the Upper Toarcian

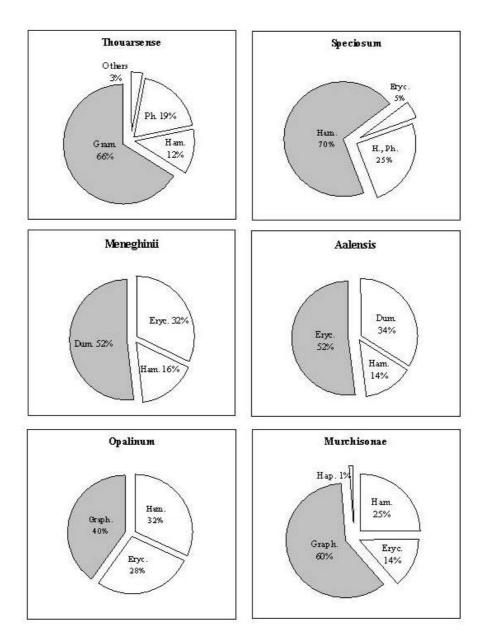


Figure 3. Proportions of Ammonitina families and subfamilies in the Upper Toarcian – Middle Aalenian (Dum. – Dumortieriinae, Eryc. – Erycitinae, Gram. – Grammoceratinae, Graph. – Graphoceratidae, H. – Hildoceratidae, Ham. – Hammatoceratinae, Hap. – Haplocerataceae, Ph. – Phymatoceratidae).

# Systematics and phylogeny

# SUPERFAMILY Hammatocerataceae Schindewolf, 1964

Genus Erycites was introduced by GEMMELLARO (1886). GÉCZY (1966:86-87) gave a detailed research history of the genus, thus it seems sufficient to summarize the results of the last forty years. One of the most important changes considered the taxonomic position of the genus. Having accepted ARKELL's interpretation (ARKELL, 1957:254) GÉCZY placed Erycites in the superfamily Hildocerataceae. Meanwhile an alternative taxonomic reconstruction was proposed by SCHINDEWOLF (1964) on the ground of analyses of the suture-line character, above all the structure of the U lobe of numerous taxa included previously in the Hildocerataceae. SCHINDEWOLF (l.c.) paid particular attention to the significant differences, and suggested a new superfamily-taxon name for the group: the Hammatocerataceae. According to him, families Hammatoceratidae (Hammatoceratinae, Dumortieriinae), Paroniceratidae, Tmetoceratidae, Oppeliidae, Phlycticeratidae) can be classified within the Hammatocerataceae. However, due to the absence of a general consensus concerning the methodology of classification (diverse interpretations of the importance of shell morphology, suture configuration, stratigraphic range and paleobiogeographic distribution by various authors), there was no agreement on the validity of the new superfamily (see TINTANT & MOUTERDE, 1981:87, MOYNE & NEIGE, 2004:115). Some authors, with slight rectification, accepted SCHINDEWOLF's conception and regarded Ervcites belonging as Hammatocerataceae (SCHLEGELMILCH, 1976, 1985, TINTANT & MOUTERDE, 1981, VENTURI, 1982, 1999, VENTURI & FERRI, 2001, RULLEAU et al., 2001, MYCZYNSKI, 2004). Without recognition of the Hammatocerataceae, WESTERMANN (1993:196) emphasized that the family Phymatoceratidae including the subfamily Hammatoceratinae (DONOVAN et al., 1981, PAGE, 2008) - was "unusually broadly defined" and its revision would be required. In VENTURI's papers (2001, 2004) it is discussed that - considering the suture-line and shell morphology remarkable differences can be demonstrated between the Hildocerataceae and the Hammatocerataceae, therefore the validity of the latter should be acknowledged.

An integrated analysis of the Jurassic – Cretaceous Ammonitida shell structure was carried out by KVANTALIANI et al. (1999). The variability of shell features concerning the suture-line character, the morphology, the sculpture and the inner structure during the ontogenesis was circumstantially treated. Accordingly, the Toarcian – Aalenian Ammonitina

phylogenetic links can be established as follows (KVANTALIANI et al., 1999:150-150):

- Eoderoceratoidea → Hildoceratoidea → Sonniniidea
- Eoderoceratoidea  $\rightarrow$  Hammatoceratoidea  $\rightarrow$  Stephanoceratoidea

RULLEAU et al. (2001:51-60) rendered a detailed interpretation of the Toarcian – Aalenian Hammatocerataceae phylogeny. Accordingly, beside morphological evidences there is a phylogenetic proof for the validity of the superfamily. Recognition of the Hammatocerataceae makes possible to connect those families (Hammatoceratidae, Ervcitidae. Graphoceratidae, Sonniniidae) which are invariably regarded as ancestors of all Middle Jurassic ammonite families. It seems a plausible hypothesis for all authors that each Bajocian Ammonitina taxon descended from those families, which otherwise should be placed within the Hammatocerataceae (e.g. DONOVAN et al., 1981, SANDOVAL et al., 2000). According to CALLOMON (1984:147), genus Erycites gave rise to subfamilies Otoitinae MASCKE and Stephanoceratinae NEUMAYR, and the following lineages were presented by WESTERMANN (1993, 1995) for the Middle Aalenian – Lower Bajocian:

- Hammatoceratinae *Planammatoceras*, *Csernyeiceras* → Strigoceratidae
- Hammatoceratinae → (independently of Strigoceratidae) Haplocerataceae (Bradfordiinae, Oppeliinae)
- Erycitinae: *Abbasites* BUCKMAN → Otoitidae: *Docidoceras cylindroides* BUCKMAN
- Erycitinae: Erycites gonionotus BENECKE, Abbasitoides modestus  $\rightarrow$  Stephanoceratinae: Riccardiceras longalvum (VACEK)

WESTERMANN's conception agrees well with those of RULLEAU et al. (2001), MOYNE & NEIGE (2004:120-121) and MOYNE et al. (2004:515). Furthermore it was completed with the presumable connection between genus *Tmetoceras* and the superfamily Spirocerataceae HYATT by CALLOMON (1980:263), PAGE (1993:217) and ROUGET et al. (2004:510).

The genus *Csernyeiceras* discussed by GÉCZY (1966:162, 1967:221) and CALLOMON & CHANDLER (1994:26) seems to have an uncertain phylogenetic position. The genus has recently been included in the revised subfamily Phlycticeratinae SPATH by SCHWEIGERT et al. (2000) and SCHWEIGERT et al. (2007). Accordingly, the following phylogenetic link was suggested for the Upper Toarcian – Aalenian times: Phlycticeratinae: *Esericeras, Phlyseogrammoceras* — *Csernyeiceras* — *Phlycticeras* — Strigoceratinae BUCKMAN: *Strigoceras praenuntium* However, the validity of the superfamily-taxon Hammatocerataceae remained controversial. Some

authors placed *Erycites* in the superfamily Stephanocerataceae NEUMAYR (WESTERMANN RICCARDI, 1979:115), or classified the erycitid group and the Hammatoceratinae within the Hildocerataceae (DONOVAN et al., 1981, WESTERMANN & RICCARDI, 1985:18, Linares & Sandoval, 1996:288, Géczy & SZENTE, 2007, PAGE, 2008). The Hammatocerataceae was also ignored by PAGE (1993, 2008) and ROUGET et al. (2004) in their taxonomic summary. According to MOYNE & NEIGE (2004), it is worth emphasizing two facts recognized by all authors. On one hand, the hammatoceratid and erycitid groups had appeared at almost the same time in the Middle Toarcian and ranged parallel with one another to the uppermost Aalenian, on the other, both groups played an essential role in the Middle Jurassic Ammonitina phylogeny.

The necessity of a general revision of the Jurassic Ammonitina systematics seems obvious for several authors (PAGE, 1993, 2008, WESTERMANN, 1993, VENTURI & FERRI, 2001, RULLEAU et al., 2001, MOYNE & NEIGE, 2004, 2007). In the present study SCHINDEWOLF's taxonomic scheme is considered to be acceptable. On the basis of the similarities concerning the morphology, the suture-line, the close stratigraphic range, and the phylogenetic relationship, attributes an important position Hammatocerataceae, i.e. as the ancestral stock of the Jurassic Ammonitina connecting the Middle Hildocerataceae and the Stephanocerataceae.

# FAMILY Erycitidae SPATH, 1928

The "Erycitidae" morpheme first appeared in SPATH's work (1928:74): "Sonninidae are also often confused with certain Ludwigids (*Bredyia*) and even offshoots of Lytoceratids (Erycitidae)". However, instead of "Erycitidae", the *Erycites* or the Erycitid forms were used discussing the *Erycites*, *Abbasites*, *Ambersites* group by the author in his later works (SPATH, 1931, 278-280, 1936:11-12). Nevertheless, on the basis of priority, it is SPATH who has recently been considered as the author of the family Erycitidae.

ARKELL (1957:267) did not regard the Erycitidae SPATH, 1928 as a valid taxon, therefore he classified genera *Erycites* and *Abbasites* within the Hammatoceratidae. This systematic conception were accepted by GÉCZY (1966), DEZI & RIDOLFI (1978), TINTANT & MOUTERDE (1981), SCHLEGELMILCH (1985), VENTURI (1981, 1982, 1994, 1999), SCHWEIGERT (1996), and VENTURI & FERRI (2001). The genus *Erycites* was included in the family Phymatoceratidae by DONOVAN et al. (1981) and CALLOMON & CHANDLER (1994), although this classification was not acknowledged by most authors.

The Erycitidae SPATH family name was reintroduced by WESTERMANN & RICCARDI (1972:93). It was first considered as a family within the Stephanocerataceae (WESTERMANN & RICCARDI,

1979:114-115) including two subfamilies: Erycitinae Erycites, Abbasites, Abbasitoides Podagrosiceratinae subfam. nov.: Podagrosiceras MAUBEUGE et LAMBERT, Arkelloceras FREBOLD, (?) Ermoceras DOUVILLÉ, ?Torrensia STURANI. Later the was placed into the Hildocerataceae (WESTERMANN & RICCARDI, 1985:18), and the Podagrosiceratinae was completed with new genera Sphaerocoeloceras JAWORSKI and Westermanniceras (RICCARDI, 2001). From the 1990s on, the Erycitidae has been assumed to be a valid family, and it was frequently used e.g. by WESTERMANN, 1993, GOY et al., 1995, LINARES & SANDOVAL, 1996, and RICCARDI, 2001. After the excellent study of RULLEAU et al., 2001, a professional consensus has been established regarding the use of the taxon (VENTURI, 2004, MOYNE & NEIGE, 2004, BECAUD et al., 2005, PALLINI et al., 2005).

#### SUBFAMILY Erycitinae SPATH, 1928

Diagnosis

Medium- or small-sized shell with either an erycitid, or a gradually growing evolute coiling. In the first case the sphaerocone and depressed inner whorls become more evolute and compressed during the ontogenesis. Whorl-section is depressed, subcircular or oval-shaped. A weakly developed keel or a smooth band forms a ventral interruption of the ribbing that disappears gradually in the last phylogenetic period of the subfamily (Abbasites, Ambersites, Abbasitoides). Ribs branch at the lower third or at the half of the whorl-height without tubercles, and fade away on the venter. Erycitid suture-line: E and ES are weakly developed, L is long, broad and ramified, LS is broad and well-developed, U is divided and oblique. Macroconch and microconch forms of several Aalenian genera have been assumed by some authors:

LINARES & SANDOVAL (1989, 1996):

- Erycites fallifax ARKELL Spinammatoceras pugnax (VACEK) (m)
- Spinammatoceras tenax (VACEK) (M) S. schindewolfi Linares et Sandoval (m)
- *Malladaites pertinax* (VACEK) (M) *M. vaceki* LINARES et SANDOVAL (m)
- Haplopleuroceras subspinatum (BUCKMAN) ?
   H. inaequalicostatum GERARD

WESTERMANN (1993:204, 1995:114):

- E. fallifax E. punctum (VACEK)
- Abbasitoides modestus (VACEK) "Coeloceras pumilus" VACEK

(The Gerecse material does not seem to provide the opportunity for a detailed research on the sexual dimorphism of the Erycitinae.)

#### Distribution

The Erycitinae is typical of the Upper Toarcian

– Aalenian of Europe, North Africa, Caucasus, Iran,
Alaska, Thailand, Tibet and New Zealand(?),

however, most species are known from the Mediterranean region (SATO, 1961, 1975, GÉCZY, 1966, NUTSUBIDZE, 1966, BRAUN & JORDAN, 1976, IMLAY, 1984, IMLAY & DETTERMAN, 1973, WESTERMANN, 1980, WESTERMANN et al., 2000, SEYED-EMAMI, 1967, 1971, SEYED-EMAMI et al., 2006, YIN, 2006). A fragmentary *Erycites* sp. was also recorded by MAUBEUGE & LAMBERT (1955, pl. 1, fig. 7) from Argentine, but according to WESTERMANN & RICCARDI (1985:18): "the late Toarcian and Aalenian Erycitinae are unknown in the Andean Province, but an offshoot of the long-ranging *Erycites*, near the root of *Abbasites*, probably gave rise to the endemic Andean *Podagrosiceras*..."

#### Remarks

**Ervcites** and subgenus **Abbasites** (=Ambersites) were classified within the subfamily Hammatoceratinae by ARKELL (1957:267). It was recognized by ELMI (1963), GÉCZY (1966), DEZI & (1978),**SCHLEGELMILCH RIDOLFI** (1985),Schweigert (1996), Venturi (1981, 1982, 1994, 1999), VENTURI & FERRI (2001), although the close relationship of genera Erycites, Abbasites and Ambersites was emphasized by LELIÈVRE (1960:35), ELMI (1963:104) and GÉCZY (1966:87). DONOVAN et al. (1981:147) considered Abbasites as a genus within the family Otoitidae.

The "Erycitinae" taxon name was first used by WESTERMANN (1964, fig. 14). The Erycitinae Spath, 1928 subfamily-taxon was erected on the ground of the Erycitidae (SPATH, 1928:74) by WESTERMANN & RICCARDI (1972:93). The validity of the subfamily was accepted by WESTERMANN & RICCARDI (1985), Westermann (1993), Callomon & Chandler (1994), LINARES & SANDOVAL (1996) and CRESTA (1997). The following genera and subgenera were placed in the Erycitinae by RULLEAU et al. (2001): "Erycites GEMMELLARO, E. (Abbasitoides) GÉCZY, Abbasites BUCKMAN, A. (Ambersites) BUCKMAN, Malladaites LINARES et SANDOVAL, Spinammatoceras SCHINDEWOLF, *Haplopleuroceras* BUCKMAN, Cagliceras gen. nov.". A new endemic genus from Iran, Shahrudites SEYED-EMAMI became recently included within the subfamily by SEYED-Emami et al. (2006). Genera Cagliceras RULLEAU et ELMI, 2001, Erycites GEMMELLARO, 1886, and Abbasitoides GÉCZY, 1966 can be documented from the Gerecse assemblage.

Papers published after the "Csernye-monograph" (GÉCZY, 1966) show a general agreement in the *Erycites* research, that integrated analyses of the shell morphology, the suture-line characters and the stratigraphic range must be taken into consideration. Works of PINNA (1968), DEZI & RIDOLFI (1978) and VENTURI (1981, 1994) are obviously characterised by this synthetic methodology. The study OF DEZI & RIDOLFI (however, the detailed species-level stratigraphic range is missing from the work) has a

further significance for the examination of the Hungarian Ammonitina fauna, because specimens presented by the authors prove a markedly close relationship with the Hungarian material. It was CRESTA (1997) who first figured the erycitid specimens of the Gemmellaro-collection, and having revised them he designated the lectotypes of *E. sutneri* and *E. barodiscus*. Moreover, the subfamily was discussed by RULLEAU (1996) and CALLOMON & CHANDLER (1994).

#### Phylogeny of the Erycitinae

The early history of the subfamily was studied by VENTURI (1975, 1981). Accordingly, the earliest representative of the Hammatocerataceae, i.e. Rarenodia latecosta VENTURI, which derived from the Phymatoceratidae, appeared in the Toarcian Falciferum Zone (cf. MOYNE & NEIGE, 2004:117). It can be thought of as the ancestor of Praerycites VENTURI, which turned up in the Bifrons Zone. Despite controversial details (e.g. presumed identity of Praerycites civitellense VENTURI Hammatoceras costatum GABILLY, see CRESTA et al., 1989:93), it seems a plausible hypothesis that all genera of the Hammatoceratinae radiating at the end of the Gradata Zone (Geczyceras, Hammatoceras, Crestaites) are direct descendants of Rarenodia and Praerycites (VENTURI & FERRI, 2001, RULLEAU et al., 2001, MOYNE & NEIGE, 2004). As the exact phylogenetic interpretation of Praerycites needs more research, it has been recently assumed that the Hammatoceratinae gave rise to the Erycitinae characterised by specific erycitid suture configuration. The earliest species belonging to the genus Cagliceras (C. picenum, C. enigmaticum n. sp., C. elaphum) occurred in the Speciosum Zone. The close relationship between the two subfamilies can be well demonstrated. Some taxa have striking morphological resemblance with different suture-line structures (Cagliceras enigmaticum n. sp. - Crestaites victorii, Cagliceras costulosum – Geczyceras porcarellense), while other species can evidently be regarded as transitional forms (Erycitoides howelli (WHITE), E. personatiformis GÉCZY, E. szontaghi PRINZ, Cagliceras enigmaticum n. sp.). The acme of Cagliceras is proved in the Upper Toarcian and around the Toarcian-Aalenian boundary.

The descendant of *Cagliceras* is the genus *Erycites*, which appeared in the uppermost Toarcian and flourished in the Aalenian stage. According to WESTERMANN (1964:66, 1993:198), the genus can be divided into two groups: the *Erycites fallifax – Abbasites* group is characterised by a sphaerocone, involute coiling, whereas the *Erycites gonionotus – Abbasitoides* group is marked by a serpenticone, planulate shell. Having created the genus *Malladaites*, LINARES & SANDOVAL (1986, 1996) proposed the following phylogenetic links of the Aalenian

Erycitinae: E. fallifax  $\rightarrow$  Spinammatoceras tenax  $\rightarrow$ Malladaites pertinax Haplopleuroceras subspinatum. CALLOMON & CHANDLER (1994:21) assumed that three radiations of Erycites can obviously be discerned. The first one occurred in the Scissum Zone with the separation of genera  $Spinammatoceras \rightarrow Malladaites \rightarrow Zurcheria$ . The second and the third radiations took place in the Murchisonae Zone, with the appearance of Abbasites and Abbasitoides. Abbasites is invariably thought of as the ancestor of the Otoitidae (Docidoceras, *Emileia*) and the Stephanoceratidae, Abbasitoides, according to WESTERMANN (1995:109) can be regarded as the earliest representative of that branch which leads to the Stephanoceratinae (Stephanoceras [Docidoceras] longalvum VACEK).

Having recognized the latter interpretation, it would be possible to reconstruct a more exact lineage of both the subcadicone Docidoceras cylindroides and the serpenticone Riccardiceras (type-spec. Coeloceras longalvum VACEK) (cf. DIETZE et al., 2001). SANDOVAL et al. (2001:32) established the following links: **Abbasitoides** Riccardiceras Stephanoceratidae: Mollistephanus, and Erycitinae: Abbasites → Otoitidae: Docidoceras → Emileia, Otoites: however, the authors included Riccardiceras within the Otoitidae. Phylogeny of the genus Mollistephanus Buckman has recently been treated by CHANDLER & DIETZE (2004). In RICCARDI's paper (2001) it is considered that the origin of the subfamily Podagrosiceratinae typical of the Andean Province can be traced in genera Abbasites or Abbasitoides.

# Systematic palaeontology

#### Abbreviations

The following abbreviations are used in this study:

E – subfamily Erycitinae

Sections: P – Pisznice, B – Bánya-hegy, G – Kis-Gerecse, TA – Tölgyhát "A", TB – Tölgyhát "B" Number of bed and capitals for indication the specimens found in the same bed.

(e.g. EP84B – specimen B belonging to the subfamily Erycitinae, Pisznice section, bed 84)

#### Abbreviations of dimensions

D – diameter, H – whorl-height, h – H/D, W – whorl-width, w – W/H, U – umbilical-width, u – U/D

#### Genus Cagliceras RULLEAU et ELMI, 2001

Type species: *Erycites elaphus* MERLA, 1934
The type species (MERLA, 1934, p. 25, pl. 4, fig. 5) was designated by RULLEAU & ELMI (RULLEAU et al., 2001:76).

#### Diagnosis

Medium-sized form with a gradually growing, evolute coiling. Umbilicus is wide and moderately deep. Whorl-section is either oval-shaped or subcircular. Ventral keel is weakly developed on the inner whorls and disappears during the ontogenesis. Strong ribbing persisting throughout the shell is interrupted on the venter. Tubercles are not characteristic. Erycitid suture-line: short E lobe, long and ramified L lobe, divided and oblique U lobe.

#### Remarks

The genus was created by RULLEAU & ELMI (RULLEAU et al., 2001:76) including erycitid taxa with specific morphological features and of Upper Toarcian range. The group was mainly described by MERLA (1934), and the significant differences from the former *Erycites* species were already emphasized by him (MERLA, 1934:22-23, 28-29). Accordingly, the new Toarcian erycitids differ

from *E. fallax* (BENECKE) and *E. reussi* (HAUER) by having more evolute coiling and relatively compressed whorl-section. The plausible separation of the group was first suggested by VENTURI (1994:348), however, without a proposal of a new taxon name ("*Erycites*" gr. *elaphus*, "*Erycites*" gr. *costulosus*, "*Erycites*" gr. *picenus*).

Five species were placed in the genus by RULLEAU & ELMI (1.c.): *C. elaphum* (MERLA), *C. rotundiformis* (MERLA), *C. robustum* (MERLA), *C. crassiventris* (MERLA) and *C. picenum* (FOSSA-MANCINI). In the present study it is considered that on the ground of morphology and stratigraphic range, three further erycitid species could be included within the genus: *C. costulosum* (MERLA), *C. enigmaticum* n. sp. and *C. banffyi* (PRINZ). *C. banffyi* has been hitherto known from Úrkút with one example (GÉCZY, 1965:26) and from Csernye with two examples (GÉCZY, 1966:94).

#### Distribution

According to RULLEAU et al. (l.c.), *Cagliceras* is typical of the Meneghinii and Aalensis Zones. However, the extended stratigraphic range of the genus has been well-documented (see below). It is known from the Upper Toarcian – Lower Aalenian of the western Tethys. Most species seem to be restricted to the Mediterranean region, only two

taxa have been recorded from the Submediterranean region: *C. elaphum* (Germany: SCHWEIGERT, 1996, France: CASSEL, 1997) and *C. picenum* (France: RULLEAU, 1996). One taxon, *C. cf. robustum* (MERLA) has been described from Iran (SEYED-EMAMI, 1967). In the Gerecse Mts, the earliest representatives of *Cagliceras* occurred in the Speciosum Zone, the genus flourished during the Meneghinii and Aalensis Zones, and disappeared in the Opalinum Zone.

Cagliceras elaphum (MERLA, 1934) (Pl. 1, fig. 1-2, 3, Pl. 2, fig. 1, Pl. 3, fig. 1, 2)

1867-1881 Ammonites reussi Hauer, Meneghini, p.56, pl. 15, fig. 1

1934 Erycites elaphus n. sp., MERLA, p. 25, pl. 4, fig. 5 ?1965 Erycites elaphus pannonicus n. subsp., GÉCZY, p. 25, fig. 4, pl. 4

1966 *Erycites elaphus* MERLA, GÉCZY, p. 97, fig. 82, pl. 28, fig. 4, pl. 42, fig. 3

1967 Erycites elaphus MERLA, BARBERA, p. 304, pl. 6, fig 2

1968 Erycites elaphus MERLA, PINNA, p. 27, pl. 3, fig. 12

1968 Erycites elaphus MERLA, GÉCZY, p. 128, pl. 4, p. 129, pl. 5, fig. 1

1969 Erycites elaphus MERLA, PINNA, pl. 5, fig. 11

1978 Erycites elaphus MERLA, DEZI & RIDOLFI, p. 51, fig. 73-74

1994 "*Erycites" elaphus* MERLA, VENTURI, pl. 6, fig. A, pl. 7, fig. 10

1995 Erycites elaphus MERLA, GOY et al., p. 102, pl. 13, fig. 2-4

1996 Erycites elaphus MERLA, SCHWEIGERT, pl. 4, fig. 1 2001 "Erycites" elaphus MERLA, VENTURI & FERRI, p. 233, fig. f-g

Material: 32 internal moulds of different state of preservation

#### Dimensions:

Dimens	ions:						
specimen	D	Н	h	W	w	U	u
EP84A	144	36	25%	32	89%	78	54%
EP92	140	34	24%	28	82%	72	51%
EG18A	138	32	23%	30	94%	74	53%
EP88	128	31	24%	22	71%	68	53%
EB11	128	30	23%	20	66%	69	54%
EP84B	114	30	26%	24	80%	60	52%
EP95A	110	29	26%	25	86%	60	54%

#### Description

Medium-sized, evolute form with a wide and moderately deep umbilicus. No umbilical edge is present. The flanks are convex, both the ventrolateral shoulder and the venter are rounded. The body chamber is slightly higher and more compressed, but – except on two examples – wider

than the penultimate whorl. The ventral keel is thin and weakly developed. The inner whorl-section is wide-oval, while the section of the body chamber is high-oval with maximum width at the lower third of the flank. The ornamentation is characterised by strong ribbing persisting up to the peristome. Short, thick, moderately prorsiradiate primary ribs emerge on the umbilical wall, their width and intercostal space are equal. The primaries grow up into pseudotubercles on several examples. The primaries become sharper, more widely spaced and more prorsiradiate on the body chamber, and the furcation zone moves up to the mid-flank. Detailed numbers of primary and secondary ribs on the last whorls of three of the examples: EP85: 27 - 75, EP81B: 28 - 61, EP95A: 33 - 75. The primaries branch into 2 or 3, rarely 4 secondary ribs at the lower third of the lateral walls. The thinner, prorsiradiate secondaries bend forward, and fade away close to the keel. The secondaries tend to be less developed on the body chamber. The length of the body chamber is 4/5 of the last whorl. The projected, oblique peristome is followed by a shallow constriction. The suture-line structure shows erycitid characters with short E and long, broad L. The L is placed close to the venter. The first lateral saddle is broad and ramified. The U2 and U3 being oblique point to the tip of the L (Figure 4)



Figure 4. Suture-line of *Cagliceras elaphum* (MERLA) (ETA24)

Remarks and comparisons

Despite the variability of the whorl-section discussed here, other features show a good agreement with MERLA's holotype (MERLA, 1934, pl. 4, fig. 5).

Due to its wide range, numerous examples are figured in the literature. It was DONOVAN (1958:58) who first emphasized the intraspecific variability of *C. elaphum*, and his observation can be proved by the materials described in various papers, as well as by the Gerecse examples. Body chambers of two specimens (EP85, EP90) are not wider than the penultimate whorl, furthermore slight variability in the ornamentation and in the whorl-section has also been detected in the material. It is worth mentioning that rather

different cross-sections have been documented in the literature. A high-oval section was described by MERLA (1934:25), a wide, highly-arched oval section was published by PINNA (1968), a wide, high, subcircular-subquadrangular section can be found at GÉCZY (1966), and a subcircular section was figured by VENTURI (1994). As for the Gerecse material, flanks of the example EG18A are flattened, so its whorl-section is considerably subquadrangular (D: 138, H: 32, W: 30). However, on the ground of the stability of other specific characteristics, the variability of the sections should be assumed a pure individual divergence. Consequently, in the present paper it is regarded that the subcircular section of Erycites elaphus pannonicus GÉCZY, 1965 (which otherwise shows close affinity to specimens of DEZI & RIDOLFI, 1978) is merely an individual feature, so the validity of this subspecies is not proved. Due to the imperfect state of preservation, it appears difficult to give a detailed interpretation of the Erycites aff. elephas [sic!] MERLA figured by EBLI (1997:39, fig. 7).

Main specific differences between *C. elaphum* and other Erycitinae taxa can be demonstrated as follows. *C. crassiventris* is a subserpenticone form with a less developed ribbing and a narrow-oval whorl-section. *C. rotundiformis* is characterised by a wider venter, a finer ornamentation and a regularly subcircular section. *C. costulosum* is a slightly more involute form with a dense and rectiradiate ribbing. *Erycites reussi* is characterised by a moderately evolute, depressed coiling with sharper ribs. *E. barodiscus* is a remarkably robust form with broader whorls and coarse sculpture. *C. elaphum* also differs from *Crestaites victorii* by being less strongly ribbed with short primaries.

#### Distribution

Italy – Valdorbia: Jurense Zone (MERLA, 1934:25), Meneghinii Zone (DONOVAN, 1958:37), Val Maone, Vallone S. Giuliano: Lower Aalenian (BARBERA, 1967:305), Alpe Turati: Upper Toarcian (VENZO, 1952:116, PINNA, 1968:28), Monte Catria and M. Nerone: Meneghinii Zone (CRESTA, 1994:115), San Severo: Meneghinii Zone (VENTURI, 1994:348), Colle d'Orlando: Meneghinii Zone (PARISI et al., 1998:22)

Spain – Colomera: Upper Toarcian (LINARES & RIVAS, 1971:195), Cerro Méndez 2. sect.: Reynesi Zone (GARCIA-GÓMEZ et al., 1994:216), Cordilleras Béticas: Reynesi Zone, Mallorca: Pseudoradiosa Zone, Aalensis Zone (GOY et al., 1995:103)

France – Gard: Gruneri Subzone (CASSEL, 1997:165)

Germany – Reutlingen: Levesquei Zone (SCHWEIGERT, 1996:6)

Hungary – Csernye: Upper Toarcian – Lower Aalenian (GÉCZY, 1966: 97), Gerecse Mts: uppermost Speciosum Zone – middle Opalinum Zone

- 1934 Erycites crassiventris n. sp., MERLA, p.26, pl. 4, fig. 1
- 1967 Erycites crassiventris MERLA, BARBERA, p. 304, pl. 6, fig.1
- 1978 *Erycites crassiventris* MERLA, DEZI & RIDOLFI, p. 53, fig. 77-78

Material: 8 relatively well-preserved internal casts and one fragmentary specimen

#### Dimensions:

specimen	D	Н	h	W	W	U	u
EP95B	146	34	23%	28	82%	80	55%
EB15A	124	28	22%	20	71%	67	54%
EP97D	124	30	24%	18	60%	74	60%

#### Description

Medium-sized, subserpenticone form with a narrow and high venter. The umbilicus is wide and shallow without umbilical margin. The flanks are gently convex on the phragmocone, and become compressed on the last whorl. The ventrolateral shoulder is rounded. On the venter of the inner whorls a weakly developed keel can be traced. The cross-section is somewhat wide-oval at the phragmocone, while the body chamber has a high, compressed, narrow-oval section, with maximum thickness at the lower third. The ornamentation consists of strong primary and more weakly developed secondary ribs. The primaries rising on the umbilical wall are rectiradiate on the inner and become distant and prorsiradiate on the body chamber. Their width and intercosta are of the same size. The primaries either bifurcate or rarely trifurcate at the lower third of the whorl. The thin secondary ribs curve forward and fade away close to the carina. The body chamber occupies the entire last whorl. The projected peristome is followed by a shallow and markedly oblique constriction. There is another radial, shallow constriction on the body chamber as well. The sutures are characterised by the specific ramified erycitid lobes, with a long and moderately wide L and a well-developed LS1. E is short and narrow, its length is 1/3 of the L. ES is divided by a relatively long and narrow accessory lobe. The presence of a significantly welldeveloped and oblique auxiliary saddle was already noted by MERLA. The U lobes are divided and also oblique, the U2 points at the tip of the L (Figure 5).

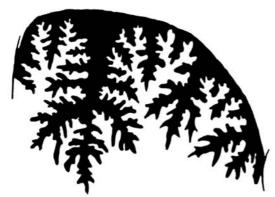


Figure 5. Suture-line of *C. crassiventris* (MERLA) (EB15A)

# Remarks and comparisons

Erycites crassiventris is a relatively rare species. For this reason, it was not regarded as a valid taxon by DONOVAN (1958:58), who considered it as only a more compressed and more evolute variation of Erycites elaphus. As opposed to this, studies of BARBERA (l.c.) and DEZI & RIDOLFI (l.c.), as well as the present paper can demonstrate again marked differences between the two taxa, consequently the validity of both species appears to be well-established.

Despite the obvious affinity between C. crassiventris specimens of the Gerecse material and MERLA's holotype (MERLA, 1934:26), there noteworthy differences in size ornamentation. One of the main morphological features of the holotype is the length of the body chamber, which is 5/4 of a whorl. However, this size has not been confirmed in the later publications. BARBERA (1967, pl. 6, fig. 1) documented a one-whorl long body chamber, while the specimens figured by DEZI & RIDOLFI (1978:53, fig. 77-78) bear body chambers only of 2/3 whorl length. As we saw, the body chamber of the adult example EP95B occupies a whole whorl. In addition to this, the disornamented body chamber was regarded by MERLA as a specific characteristic of the taxon. This morphological feature has been confirmed neither. The sculpture remains of the same style both on the phragmocone and on the body chamber of specimens figured by BARBERA (l.c.) and DEZI & RIDOLFI (l.c.). The Gerecse material displays the same characteristic. A well-preserved specimen (EB15A) possessing only half of the body chamber, however, resembles well the holotype. ornamentation becomes suddenly developed on the phragmocone, at the half of the penultimate whorl, and tends to fade on the body chamber.

In view of the coiling, the whorl-section and the sculpture the *Erycites* cfr. *fallifax* ARKELL figured by DEZI & RIDOLFI (1978, p. 52, fig. 75) may represent a *C. crassiventris* specimen.

#### Distribution

Italy – Montagna della Rossa: Upper Aalenian (MERLA, 1934:27), Fonte S. Giglio: Meneghinii Zone (DONOVAN, 1958:38), Sella dei due Corni: Lower Aalenian (BARBERA, 1967:304), Monte Catria and M. Nerone: Aalensis Zone (CRESTA, 1994:115)

Spain – Sierra Sagra: Upper Aalenian(?) (FOUCAULT, 1971:143)

Hungary – Gerecse Mts: Speciosum and Meneghinii Zones

# Cagliceras robustum (MERLA, 1934) (Pl. 5, fig. 4)

1934 Erycites robustus n. sp. MERLA, p. 25, pl. 2, fig. 6 a-b, pl. 3, fig. 7

1966 Erycites cf. robustus MERLA, GÉCZY, p. 97, fig. 83, pl. 28, fig. 1

1967 Erycites cf. robustus Merla, Seyed-Emami, 1967, p. 98, pl. 3, fig. 13

1978 Erycites robustus MERLA, DEZI & RIDOLFI, p. 50, fig. 69-72

Material: 4 internal moulds of mediocre preservation

# Dimensions:

specimen	D	Н	h	W	W	U	u
EG18B	104	30	29%	30	100%	54	52%
EP89A	90	26	29%	24	92%	47	53%
EP88B	90	26	29%	26	100%	46	51%

# Description

Medium-sized form of moderately evolute coiling with a wide and gradually deepening umbilicus. There is no edge between the umbilical and lateral walls. The flanks are convex, the venter is low and broadly arched. There is a low, thin, weakly developed carina in the middle of the ventral part. The whorl-section of the inner whorls is subcircular, becoming wide-oval on the last whorl. Its maximum width is a little below the medium whorl-height. The ornamentation consists of strong primary and finer secondary ribs. The primaries emerge from the umbilicus, and develop into radially elongated, projected nodes with concave intercosta at the lower third of the flank. Their width and interspace are of the same size. The example EP88B bears 24 primary ribs on the last whorl. The primaries bifurcate at the lower third on the inner whorls, while the furcation points lie at the half of the flank on the last whorl. The thinner secondaries are slightly prorsiradiate. They bend forward on the venter and fade away close to the keel. Intercalatory ribs appear between the secondaries on the last whorl. No whole body chambers are preserved. The suture-line shows an erycitid character. The length of the weakly developed E is 1/3 of the relatively wide and long L, the umbilical lobes are oblique. The LS1 is significantly ramified, the well-developed auxiliary saddle is also oblique and asymmetrical.

#### Remarks and comparisons

The example EP88B figured here seems to agree well with MERLA's type (1934, pl. 2, fig. 6). The characteristic bullate sculpture makes *C. robustum* easily distinguishable from other *Cagliceras* species.

#### Distribution

Italy – Montagna della Rossa: Upper Toarcian (MERLA, 1934:26), Alpe Turati: Upper Toarcian (VENZO, 1952:116)

Iran – Kerman: Upper Toarcian (SEYED-EMAMI, 1967:98)

Portugal – *C.* cf. *robustum*: Sao Giao: Mediterraneum Subzone (ELMI et al., 2007:119) ?Spain – *Erycites* cf. *robustum*: Maranchón:

Aalenian (GOY & ALFÉREZ, 1974:2)
Hungary – Csernye: Unper Tograian (GÉCZ

Hungary – Csernye: Upper Toarcian (GÉCZY, 1966:98), Gerecse Mts: Meneghinii to Opalinum Zones

Cagliceras rotundiformis (MERLA, 1934) (Pl. 5, fig. 1, 3)

1934 Erycites rotundiformis n. sp., MERLA, p. 24, pl. 3, fig. 6

1966 *Erycites* cf. *rotundiformis* MERLA, GÉCZY, p. 99, fig. 85, pl. 28, fig. 2, pl. 42, fig. 5

1968 Erycites rotundiformis MERLA, PINNA, p. 30, pl. 2, fig. 23, pl. 3, fig. 1

? 1978 Erycites cfr. rotundiformis MERLA, DEZI & RIDOLFI, p. 55, fig. 81

Material: 4 internal casts of mediocre preservation

#### Dimensions

specimen	D	Н	h	W	W	U	u
EG41A	93	28	30%	28	100%	43	46%
EG31B	80	27	33%	24	89%	35	44%
EG38A	78	25	32%	25	100%	34	43%

#### Description

Medium-sized, evolute, gradually growing shell. The umbilicus is wide and deep, the

umbilical wall steep and convex. There is neither umbilical margin nor ventrolateral edge. The flanks are rather convex, the ventral part is broad, low and rounded. The whorl-section is subcircular with maximum width at the mid-flank. No whole body chambers are preserved. The ornamentation consists of regular, well-developed ribbing interrupted on the venter by a wide smooth band. The ribbing style is continuous throughout the shell. Straight, radiate primary ribs rise on the umbilical wall, their width and intercosta are equal-sized. The primaries reaching the lower third of the flanks become gently broader, and trifurcate a little under the mid-whorl position without any tubercles. The last whorl bears 28 primaries. The less developed secondary ribs are slightly flexuous. The secondaries bend forward on the venter, and fade away in the middle. The erycitid suture-line is characterised by a short E with 1/3 length of the L. The asymmetric L is narrow, long and ramified. The trunk of the first lateral saddle is considerably narrow. The auxiliary saddle is welldeveloped, its height is about 2/3 of the LS1. The U lobe is divided and oblique, the U2 points at the tip of the L (Figure 6).



Figure 6. Suture-line of *C. rotundiformis* (MERLA) (ETA23B)

# Comparisons

The Gerecse examples are well comparable with both the holotype (MERLA, 1934:24, pl. 3, fig. 6) and the specimen presented by PINNA (1968, pl. 2, fig. 23, pl. 3, fig. 1). It is worth mentioning that those three whorl-sections described by MERLA, PINNA and GÉCZY (1966:99, fig. 85) seem to show slight differences which can be, however, considered as intraspecific variability. As opposed to this, the section of the *E. cfr. rotundiformis* figured by DEZI & RIDOLFI (1978: p. 55, fig. 81) appears significantly different from that of the holotype by having flattened lateral walls and a highly-arched ventral area.

The sculpture style and the cross-section make *C. rotundiformis* well distinguishable from the similar taxa. *C. robustum* bears bullate primary

ribs, while *C. costulosum* is more finely ribbed. The primaries of *C. elaphum* are shorter and prorsiradiate branching at the lower third of the flank. The section of the latter is high-oval on the last whorl. *C. rotundiformis* was already compared with *E. reussi* by MERLA (1934:24), accordingly, the latter is characterised by a more depressed section, a coarser ribbing and a symmetric L lobe.

#### Distribution

Italy – Valdorbia, Cagli: Jurense Zone (MERLA, 1934:24), Alpe Turati: Meneghinii Zone (PINNA, 1968:31), M. La Pelosa: Erbaense Zone (P. sternale Subzone) – Meneghinii Zone (NICOSIA & PALLINI, 1978:268), Monte Catria and M. Nerone: Meneghinii Zone (CRESTA, 1994:115)

Spain – Zegri Norte: Opalinum Zone (GARCIA-GÓMEZ et al., 1994:217)

Hungary – Csernye: Upper Toarcian – Lower Aalenian (GÉCZY, 1966:100), Gerecse Mts: Meneghinii and Aalensis Zones

# Cagliceras costulosum (MERLA, 1934) (Pl. 6, fig. 1, 2)

- 1934 Hammatoceras costulosum n. sp., MERLA, p. 13, pl. 1, fig. 3-4
- 1968 Erycites costulosus (MERLA), PINNA, p. 29, pl. 2, fig. 5
- 1978 Erycites costulosus (MERLA), DEZI & RIDOLFI, p. 46, fig. 58-63
- 1994 "Erycites" gr. costulosus (MERLA), VENTURI, pl. 6, fig. c
- 1995 Geczyceras costulosum (MERLA), GOY et al., p. 100, pl. 12, fig. 1

Material: 2 internal casts of medium state of preservation

### Dimensions

specimen	D	Н	h	W	w	U	u
EP84C	92	26	28%	22	84%	45	49%
EP84D	71	22	31%	18	82%	35	49%

#### Description

Medium-sized form with moderately evolute coiling. The umbilicus is slightly narrow and deep on the inner whorls becoming gradually wider during the ontogenesis. The umbilical wall is low, both the umbilical and the ventrolateral margins are rounded. The flanks are gently convex, the venter is slightly high and rounded with a thin, smooth intersection in the middle. The cross-section is high-oval with maximum width at the lower third. The last whorl is somewhat compressed, although it remains wider than the penultimate whorl. The ornamentation is

characterised by moderately strong primary and weakly developed secondary ribs. The primaries emerging from the umbilical margin are rectiradiate. They are dense on the inner whorls with equal width and space, but become more widely spaced on the last whorl. There are 28 primary and 84 secondary ribs on the last whorl of the example EP84C. The primaries regularly trifurcate at the lower third of the flanks. The thin secondaries are curved gently forward on the inner whorls, while they are radiate on the last whorl. Having reached the ventral interruption without fading they suddenly terminate. No whole body chambers are preserved. Although the suture-lines are not visible in all details, the structure of the characteristic erycitid lobe can be observed. The length of the weakly developed E is 1/3 of the relatively narrow L, the lateral saddle is broad, and the U is oblique.

### Remarks and comparisons

MERLA (1934:13) classified the new species within the genus *Hammatoceras*. As opposed to this, PINNA (1968:29) - having accepted GÉCZY's proposal (1966), which emphasized the priority of the suture-line analysis rather than that of the morphological features in distinguishing Erycites and Hammatoceras - revised the original classification, and, based on the suture structure, placed the taxon in Erycites. However, the taxonomic interpretation remained uncertain. In three later papers, without any explication, the species was referred to again as a taxon belonging to the Hammatoceratidae: H. costulosum MERLA (ELMI et al., 1974, pl. 4, fig. 3), Geczyceras costulosum (PETTINELLI et al., 1997, pl. 3, fig. 6, but Hammatoceras [sic!] costulosum MERLA, 1934, p. 109), and Geczyceras costulosum (MERLA) (GOY et al. 1995, pl.12, fig 1). For the coiling style, the sculpture (e.g. absence of the hammatoceratid umbilical tubercles), and, above all, for the specific suture configuration, it appears better supported to classify the taxon within the Erycitinae. Furthermore, as the morphological features and the stratigraphic range correspond to the criteria of Cagliceras, in the present study the species is considered as a member of the latter genus.

The morphological affinity is very close between the example EP84C figured here and MERLA'S holotype (1934:13, pl. 1, fig. 3-4), as well as specimens presented by DEZI & RIDOLFI (1978:46, fig. 58-63). In view of the small size (D: 41) the *Erycites costulosus* figured by PINNA (1968, pl. 2, fig. 5) seems to be a fragmentary specimen preserving only the more involute inner whorls. On the other hand, the *Geczyceras costulosum* presented by GOY et al. (1995, pl. 12,

fig. 1) slightly differs from the holotype by possessing somewhat less evolute shell as well as coarser ribbing. The Hammatoceras aff. costulosum figured by ELMI et al. (1974, pl. 4, fig.3) shows more significant differences. It is characterised by an involute shell with narrow umbilicus, by long primary ribs and subtriangular whorl-section. The example rather resembles Geczyceras porcarellense (BONARELLI, 1899) in morphology, but the suture-line is unknown. Due to the imperfect state of preservation, it seems uncertain to give an exact interpretation of either the Geczyceras costulosum figured by PETTINELLI et al. (1997) or the Erycites costulosus presented by VENTURI (1981, pl. 1, fig. 8).

A detailed comparison between *H. costulosum* and *H. porcarellense* were already described by MERLA (1934:13). Accordingly, there are specific differences between the two forms. The whorlsection of *H. porcarellense* is wider oval, its ribbing is prorsiradiate with secondaries emerging from umbilical tubercles, and its suture-line shows a specific hammatoceratid structure. Considering other similar taxa, *C. costulosum* differs from *C. elaphum* by possessing radiate and fine ribbing, it differs from *C. rotundiformis* by having ovalshaped whorl-section, and it differs from *C. robustum* by having no bullate ribbing.

# Distribution

Italy – Montagna della Rossa: Jurense Zone (MERLA, 1934:13), Fontana Longarino: Jurense Zone (MAXIA, 1943:97), Alpe Turati: Upper Toarcian (VENZO, 1952:116, PINNA, 1968:30), M. La Pelosa: Meneghinii Zone (NICOSIA & PALLINI, 1977:268), M. Subasio: Erbaense Zone (VENTURI, 1981:88), Monte Nerone: "Erbaense" Zone (CECCA et al., 1990:96), Speciosum Zone (CRESTA, 1994:115), Passo del Furlo: Meneghinii Zone (VENTURI, 1994:348)

Spain – Mallorca: Pseudoradiosa Zone, Aalensis Zone (Goy et al., 1995:98-100)

?France – H. sp. aff. costulosum MERLA: Dome de Remollon: Jurense Zone (GARIEL, 1961:704)

Hungary - Gerecse Mts: Aalensis Zone

Cagliceras picenum (FOSSA-MANCINI, 1915) (Pl. 4, fig. 1-2, Pl. 5, fig. 2)

1867-1881 *Ammonites insignis* SCHÜBLER, MENEGHINI, p. 56, pl. 13, fig. 2

1914 Hammatoceras picenum n. sp., FOSSA-MANCINI, p. 73

1934 Erycites picenus (FOSSA-MANCINI), MERLA, p. 28, pl. 4, fig. 3-4

1969 Erycites picenus (FOSSA-MANCINI), PINNA, pl. 5, fig. 4

1978 Erycites picenus (FOSSA-MANCINI), DEZI & RIDOLFI, p. 48, fig. 64-65

1994 *"Erycites"* gr. *picenus* (Fossa-Mancini), Venturi, pl. 7, fig. 2-3

1996 *Erycites* aff. *picenus* (FOSSA-MANCINI), RULLEAU, p. 6, pl. 21, fig. 4

1997 *Praerycites picenus* (FOSSA-MANCINI), PETTINELLI et al., pl. 3, fig. 4

2001 "Erycites" picenus (FOSSA-MANCINI), VENTURI & Ferri, p. 233, fig. h-m

Material: 5 internal moulds of mediocre state of preservation

#### Dimensions

specimen	D	Н	h	W	W	U	u
EG54	86	22	25%	20	91%	44	51%
EB15B	80	21	26%	20	95%	47	58%

#### Description

Medium-sized, evolute form with a gradually growing shell, and a wide and slightly deep umbilicus. Both the umbilical edge and the ventrolateral shoulder are rounded, the lateral walls are convex. The venter is moderately high and rounded. A well-defined, thin and low carina is present on the ventral part. The cross-section is wide-oval, approximately subcircular. The last whorl being not compressed is wider than the penultimate. Regular, coarse ribbing persists on the whole coiling, and consists of short, radiate primary ribs that rise on the umbilical slope with the same width and interspace. The primaries become slightly thicker, and bifurcate on the lower third of the flanks. The thinner, sharp and moderately sigmoid secondary ribs bend forward on the venter and, alternating on the two sides, reach the keel. The example EG53A bears 38 secondaries on the last half whorl. The apertural part is missing on all specimens. The suture-lines are poorly preserved, however the length of the E, which is about half of the L, can be observed.

# Remarks and comparisons

The specimens figured in the literature show a striking resemblance, apart from those of DEZI & RIDOLFI (1978:48, fig. 64-65), which gently differ from the holotype by bearing some trifurcating ribs. The agreement between the Gerecse examples and the holotype designated by FOSSA-MANCINI (1915:73) is also very close.

Both Merla (1934:28) and Géczy (1966:121) draw particular attention to the morphological affinity of *C. picenum* and *Erycites gonionotus* (BENECKE). According to GÉCZY, the specific differences can be summarised by the position of the bifurcation points, by the presence of the

intercalatory ribs and by the suture-line structures. Furthermore, the stratigraphic range of these taxa is also different. Contrary to *C. picenum* ranging in the Upper Toarcian, *E. gonionotus* has been recorded from the Murchisonae Zone of the Mediterranean region.

#### Distribution

Italy – Montagna della Rossa: Upper Toarcian (FOSSA-MANCINI, 1915:237), Cagli: Toarcian Stage (MERLA, 1934:29), Valdorbia: Insigne Zone (CRESTA et al., 1989:91), Valdorbia, F. Burano: Erbaense Zone (VENTURI, 1994:348), Monte Catria and M. Nerone: Speciosum Zone (CRESTA, 1994:115), Umbria-Marchean Basin: Gradata Zone (PETTINELLI et al., 1995:108)

Spain – Cerro Méndez 2. sect.: Reynesi Zone (GARCIA-GÓMEZ et al., 1994:216)

Portugal – Alvaiazere: D. levesquei Zone – P. aalensis Zone (MOUTERDE & RUGET, 1967:163)

France – Belmont: Pseudoradiosa Zone (RULLEAU, 1996, pl. 6)

Hungary - Gerecse Mts: Speciosum Zone

Cagliceras enigmaticum n. sp. (Pl. 6, fig. 3-4, Pl. 7, fig. 1, 2-3)

1978 Erycites aff. picenus (FOSSA-MANCINI), DEZI & Ridolfi, p. 49, fig. 66-68
1978 Erycites n. sp?, DEZI & RIDOLFI, p. 58, fig. 86-87
?1996 Hammatoceras sp., RULLEAU, pl. 20, fig. 3

Holotype: EP98 (Pl. 7, fig. 2-3), paratypes: EP97C, EB16 (Pl. 6, fig. 3-4, Pl. 7, fig. 1)

Derivation of name: The name refers to the unusual morphology, which presents a combination of the erycitid and hammatoceratid characters.

Type horizon: Speciosum Zone

Type locality: Pisznice quarry near Süttő,

Gerecse Mts

Material: 3 internal casts of mediocre preservation

# Dimensions

specimen	D	Н	h	W	W	U	u
EP98	105	24	23%	20	83%	55	52%
EP97C	100	25	25%	22	88%	55	55%
EB16	100	25	25%	20	80%	55	55%

### Diagnosis

Subserpenticone, compressed, gradually growing shell with nearly radiate, broad constrictions. Weakly developed carina, wide and shallow umbilicus, oval-shaped section. Coarse,

regularly bifurcating ribbing without tubercles. Erycitid suture-line.

#### Description

Medium-sized, subserpenticone form with gradually growing whorls. The umbilicus is wide and shallow without umbilical margin. The flanks gently convex, almost flattened, the ventrolateral edge is rounded. The venter is narrow and slightly convex with a thin and low keel. The whorl-section is oval-shaped, its maximum thickness is at the lower third of the flank. The bigger parts of the body chambers are present on two examples, apertures are missing. There are at least two moderately deep and straight constrictions on the lateral side of the body chamber. The constrictions wider than the interval of two primary ribs are radial or slightly prorsiradiate. The first is placed at 15-45 mm from the last chamber, the second is at 1/3 or a half whorl. The ornamentation characteristic on the whole shell consists of coarse ribbing without tubercles. Thick, radiate primary ribs emerge on the umbilical wall, and regularly bifurcate at the lower third of the flank. The width of the primaries is the same as the intercostal space on the phragmocone, but the ribs become widely spaced on the body chamber. There are 37 primaries on the last whorls of both the holotype and the paratype EB16. The gently thinner secondary ribs are moderately sinuous and they curve forward on the venter. Having reached the keel alternating on the two sides, the secondaries terminate. No intercalatories are present. Due to the slightly corroded surface, the suture-line is not visible in all details, however some parts of the lobes can be traced. The length of the E is about 2/5 of the long and ramified L, the external saddle is less developed than the lateral saddle, and the U lobe is divided and oblique.

#### Remarks

The new species combines the specific morphological features of two related subfamilies, the Hammatoceratinae and the Erycitinae. On the basis of the suture-line structure the species could be classified within the latter subfamily; in view of the size, the ornamentation and the coiling style it may belong to the genus Cagliceras. One of the main characteristics of the new taxon is the relatively wide and deep constriction that occurs repeatedly on the shell. This kind of constriction, which otherwise is typical of Crestaites victorii (HAHN, 1910:387), appears frequent not only on hammatoceratid, but also on erycitid forms of the Italian material described by DEZI & RIDOLFI (1978:10, 58). According to the authors, the constriction should be regarded as a specific characteristic of a new taxon, which, however, was not introduced in their study.

The especially rare C. enigmaticum n. sp. is probably a connecting form that relates the early hammatoceratid Geczyceras and Crestaites to their presumed collateral descendant, the early erycitid Cagliceras. Thus the species seems to fill a gap between Crestaites victorii and Cagliceras picenum. By reason of the biostratigraphic evaluation of the Mediterranean Ammonitina faunas in various papers, the coeval range of the first representatives of the latter genera in the lower Upper Toarcian can be noted as a wellestablished fact (Italy: Erbaense Zone: VENTURI, 1994, PETTINELLI et al., 1997, Insigne Zone: CRESTA, 1994, CRESTA et al., 1989, Hungary, Gerecse Mts: Speciosum Zone: GÉCZY, 1985a, 1985b, and see: BECAUD et al., 2005). The bed-bybed occurrences of the Hammatocerataceae taxa in the Upper Toarcian Gerecse material show the same results (Tables 1-2).

#### Comparisons

C. enigmaticum is very close in size and style of coiling to Geczyceras perplanum, but the latter bears lateral tubercles as a specific distinctive feature. C. picenum is also a strikingly similar form, but differs from C. enigmaticum by having a wide-oval or subcircular cross-section and by the lack of constrictions.

Though Crestaites victorii possesses a more robust shell, it is significantly similar in morphology to Cagliceras enigmaticum. Crestaites victorii was thoroughly investigated by Bonarelli (1899), Hahn (1910), Fossa-MANCINI (1914), GÉCZY (1965), PINNA (1968), DEZI & RIDOLFI (1978), ELMI & RULLEAU (1991), and MARTINEZ (1992). The whorl-sections, the sculptures (shape of ribbing, absence of tubercles at the furcation points) and the constrictions of both forms show close resemblance. Furthermore, the sutures are also similar, the lobe structure of C. victorii with short E and narrow L is close to that of the Erycitinae (GÉCZY, 1965:21, 1966:64, MARTINEZ, 1992:96). On the other hand, there are considerable differences between the two taxa in the coiling style and the ornamentation. C. victorii is characterised by a slightly more involute shell with h: 27-33% as well as wider whorls. Cagliceras enigmaticum is more finely ribbed with regular bifurcation, and the intercalatory ribs can be traced on the inner whorls of Crestaites victorii are absent.

On the ground of the size, the shape, the ribbing and the presence of constrictions, the agreement between the *Hammatoceras* sp. figured by RULLEAU (1996, pl. 20, fig. 3) and the holotype of *C. enigmaticum* is markedly close, however the

suture-line of the former specimen is unknown. This example was recorded from the Pseudoradiosa Zone, as both *Cagliceras* and *Crestaites* appear later in the Submediterranean than in the Mediterranean region: both genera seem to be typical of the uppermost Toarcian in the French material (ELMI & RULLEAU, 1991, RULLEAU, 1996, RULLEAU ET AL., 2001, BECAUD et al., 2005), however a *Hammatoceras* aff. *victorii* was recorded from the Bingmanni Subzone by Becaud (2006:37).

#### Distribution

Italy – Monte Carcatora: ?Sternale Subzone – Meneghinii Subzone (DEZI & RIDOLFI, 1978, pl. 1)

?France – Belmont: Pseudoradiosa Zone (RULLEAU, 1996, pl. 20)

Hungary - Gerecse Mts: Speciosum Zone

#### GENUS Erycites GEMMELLARO, 1886

Type species: *Erycites fallifax* ARKELL, 1957
The holotype of *Erycites fallifax* (*Ammonites fallax*, BENECKE, 1865, pl. 6, fig. 1) as the type species of genus *Erycites* was designated by ARKELL (1957, p. L267, fig.308.3).

#### Diagnosis

Medium-sized form with subcadione, wideoval, subcircular, subquadrangular or oval-shaped whorl-section. Either gradually growing, moderately evolute or erycitid coiling. The latter is characterized by sphaerocone and depressed inner whorls becoming more evolute and compressed on the body chamber. Either weakly developed carina or smooth band on the venter. Coarse or weaker, branching ribbing with ventral interruption. Erycitid suture-line: short E, weakly developed external saddle, long, widely ramified L, broad lateral saddle, divided and oblique U.

# Distribution

The genus is typical of the Upper Toarcian -Aalenian of Europe, but its more extended horizontal range has also been well-documented. E. fallifax, E. f. excavatus, E. gonionotus, E. baconicus, E. cf. involutus, E. personatiformis, E. banffyi and E. telegdirothi are recorded from North Africa (GARDET & GÉRARD, 1946:27-35, Lelièvre, 1960:37, DUBAR et al., 1971:401, ELMI, 1986: 232-233, SADKI, 1996:127), however the presence of the latter two species in Africa needs more evidence. E. fallifax, E. tenax and E. barodiscus are known from the Caucasus (see 1961:108-109, KRYMHOLZ, NUTSUBIDZE, 1966:150-151), and E. barodiscus from the Crimea as well (IPPOLITOV et al., 2008). Furthermore, a single *E.cf. fallifax* is recorded from Thailand (BRAUN & JORDAN, 1976:27), as well as an ?*E.* aff. *fallifax* from New Zealand (WESTERMANN et al., 2000:45). The taxon also occurs in Iran, *E. brevispira* MERLA and *E. spathi* n. sp. were described by SEYED-EMAMI (1967:98-99, 1971:36), and *E.* aff. *sphaeroconicus* BUCKMAN by SEYED-EMAMI et al. (2008:255). The genus is also documented from the Aalenian of Tibet (YIN, 2006:223).

The Csernye material is immensely rich in erycitid specimens. Beside those that have recently been classified within Cagliceras, numerous other Erycites taxa were also presented by GÉCZY (1966) as follows: E. reussi HAUER, E. cf. leptoplocus VACEK, E. intermedius HANTKEN in PRINZ, E. retrorsicostatus HANTKEN in PRINZ, E. baconicus HANTKEN in Prinz, E. telegdirothi PRINZ, E. partschi PRINZ, E. involutus PRINZ, E. szontaghi PRINZ, E. fallifax fallifax ARKELL. The author introduced several new taxa: E. personatiformis n. sp., E. telegdirothi amplus n. subsp., E. telegdirothi prorsicostatus n. subsp., E. mouterdei n. sp., E. subquadratus n. sp., E. reussi cestiferiformis n. subsp., E. ovatus n. sp., E. ovatus? rogeri n. subsp., E. fallifax excavatus n. subsp., E. fallifax flexuosus n. subsp., E. fallifax arkelli n. subsp.

The recent revision of the Gerecse material made it possible to describe the following species: *E. ovatus* GÉCZY, *E. intermedius* HANTKEN in PRINZ, *E. fallifax* ARKELL, *E.* sp. aff. reussi (HAUER), *E. barodiscus* GEMMELLARO, *E. subquadratus* GÉCZY, *E. gerecsensis* n. sp. Furthermore, a single *E.* sp. aff. telegdirothi amplus GÉCZY has been recently presented from the Kis-Teke-hegy section. In the Gerecse Mts the earliest representatives of *Erycites* (*E. ovatus*, *E. barodiscus*) occur in the upper part of the Meneghinii Zone, and the genus showing a noteworthy diversity persisted into the upper Murchisonae Zone.

#### Remarks

After the "Csernye-monograph" (GÉCZY, 1966) the genus was thoroughly examined by PINNA (1968), DEZI & RIDOLFI (1978), VENTURI (1981, 1994) and PALLINI et al. (2005). These studies rendered excellent contributions to the detailed knowledge of the evolutionary lineage and the Mediterranean stratigraphic range of Erycites. In the 1990s, a new species, Erycites exulatus sp. nov. was created by CALLOMON & CHANDLER (1994), however its validity was rejected by CRESTA (1997, 2002). Having been erected the genus Cagliceras by RULLEAU & ELMI (2001), the stratigraphic range of Erycites has been

restricted to the uppermost Toarcian Aalensis Zone and the Aalenian Stage.

*Erycites ovatus* Géczy, 1966 (Pl. 8, fig. 1, 2-3, Pl. 9, fig. 1, 4, Pl. 10, fig. 3)

1966 Erycites ovatus n. sp., GÉCZY, p. 104-105, fig. 91, pl. 30, fig. 1, pl. 42, fig. 10

Material: 15 relatively well-preserved internal moulds

#### Dimensions

specimen	D	Н	h	W	W	U	u
EP78A	125	34	27%	25	73%	59	47%
EP83B	114	29	25%	24	82%	54	47%
EG9	114	31	27%	24	77%	52	45%
EP64B	114	33	29%	24	73%	50	44%
EP78B	112	34	30%	24	70%	52	46%
EP79A	110	34	31%	24	70%	45	41%
EG7A	106	29	27%	18	62%	48	45%

#### Description

Medium-sized, evolute shell with a moderately deep umbilicus on the inner whorls becoming gradually wider and shallower during the ontogeny. The height and width of the whorls grow gradually, thus the body chamber is also higher and wider than the penultimate whorl. The umbilical wall is steep and convex on the phragmocone, while low and less convex on the body chamber. Both the umbilical and the ventrolateral margins are rounded. The flanks on the inner whorls are convex becoming flattened on the body chamber. The venter is broad, low and rounded on the phragmocone, while high and narrow on the last whorl without any keel. The inner cross-section is wide-oval with maximum width at the umbilical margin, while the section is highly-arched oval on the body chamber with maximum width at the lower third of the flank. The length of the body chamber is 3/4 of a whorl. The peristome is strikingly prorsiradiate with a projected edge and a shallow constriction behind. The ornamentation is characterized by weakly developed, prorsiradiate ribbing. The primary ribs rise from the umbilical wall on the phragmocone, and trifurcate at the lower third of the whorl with equal width and intercosta. On the body chamber primaries emerge from the umbilical edge, and become twice as widely spaced as their intervals. There are about 27 thick primaries on the last whorl. The fine secondary ribs are straight and prorsiradiate, and fade away close to the ventrolateral shoulder. Secondaries are hardly visible on the body chamber. On the whole, the

suture-line has an erycitid character, apart from the length of the E lobe, which is half of the L. The structures of the external saddles, the broad and ramified L lobes, and the oblique U lobes show great similarity in the entire *E. ovatus* material. However, on the ground of the constructions of the first lateral and the auxiliary saddles the sample can be divided into two groups. In the first group (EP83D, ETA25B, EP79A, EG31C) the bases of the saddles are broad and gently widely placed (Figures 7, 8), while in the second (EG9, EP79B) group the saddles have almost the same base (Figure 9). The latter resembles the suture-line of the holotype (GÉCZY, 1966: pl. 42, fig. 10).



Fig. 7. Erycites. ovatus GÉCZY (EG31C)



Fig. 8. Eerycites ovatus GÉCZY (EP83D)



Fig. 9. Erycites ovatus GÉCZY (EG9)

#### **Comparisons**

The Gerecse examples show sufficient agreement with GÉCZY's holotype (1966, pl. 30, fig. 1), however, slight intraspecific morphological variabilities relating to the style of the coiling, the whorl-section, and the suture-line configuration can be traced as well.

The shell form of *E. ovatus* is similar to that of E. intermedius, but there are noteworthy differences in the sculpture, and in the presence of the ornamentation on the body chamber. E. ovatus closely resembles E. fallifax by having an umbilicus becoming gradually wider, a ribbing becoming widely spaced on the body chamber, and a highly-oval section. The two taxa differ in the size, in the cross-section of the penultimate whorl, and in the suture construction. The L lobe of E. fallifax is less developed and less ramified. The diameter of an adult *E. fallifax* is never more than 100 mm, and its section of the penultimate whorl is more depressed than that of E. ovatus. Above all, as the major specific difference, the body chamber of the latter is always wider than the penultimate whorl.

 $E.\ ovatus$  shows the nearest affinity to  $E.\ sutneri$  GEMMELLARO, 1886 – there is an undoubted relationship between the two taxa. Their sizes are about the same, whorls are compressed, ornamentations are almost identical, suture-lines are very similar (E = 1/2 L). However, several specific morphological differences can be measured in the average dimensions and the whorl-sections.

Specimens of the two species with the same diameters differ from each other in the ratio of U/D and W/H.

- 1. The coiling of *E. ovatus* is sligthly more evolute:
  - the average U/D of *E. sutneri*: 0.395
- the average U/D of *E. ovatus* of Csernye: 0.426, of Gerecse: 0.457
- 2. The whorl-section of the inner whorl is depressed on *E. sutneri* (CRESTA, 1997:44, fig. 13/G, 2002:198), while it is compressed on *E. ovatus* (GÉCZY, 1966:105).
- 3. The section of the body chamber of *E. ovatus* is more compressed:
- the average W/H of the Csernye examples: 0.68, of the Gerecse examples: 0.71
  - the average W/H of *E. sutneri*: 0.795

#### Remarks

The taxon has only been cited three times in the literature, without any photos (PINNA, 1968:33-34, pl. 2, fig. 27: *E.* cf. *ovatus* GÉCZY, LINARES & RIVAS, 1971:194: *Erycites* sp. gr. *E. ovatus* (GECZY), CECCA et al., 1990:101: *E.* aff. *ovatus* Géczy). Furthermore, the cross-section

figured by Pinna differs from the holotype by being wide oval-shaped, consequently, it rather resembles *E. sutneri*.

Based on the close morphological affinities between the two forms, as well as on the lack of reliable citations, CRESTA considered *E. ovatus* GÉCZY as the junior synonymy of *E. sutneri* GEMMELLARO (CRESTA, 1997:42, 2002:199). However, the Gerecse material with its numerous well-preserved specimens ensures an excellent possibility for an exact comparison of the discussed taxa. The result does verify the fact that the morphological differences are specific ones, thus in the present paper *E. ovatus* is regarded as a valid taxon.

#### Distribution

Hungary – Csernye: Upper Toarcian – Lower Aalenian (GÉCZY, 1966:105), Gerecse Mts: Meneghinii to Murchisonae Zones

*E. sutneri* is known from the Lower Aalenian of various localities in the Apennines (CRESTA, 1997:42).

Erycites barodiscus GEMMELLARO, 1886 (Pl. 10, fig. 1, 2, Pl. 11, fig. 3)

1874 *Ammonites gonionotus* (BENECKE), DUMORTIER, p. 267, pl. 56, fig. 5-7

1886 *Hammatoceras (Erycites) barodiscus*, GEMMELLARO, p. 206

? 1935 Erycites gonionotum BENECKE, ROMAN, pl. 1, fig. 8

1966 *Hammatoceras (Erycites) fallax* Benecke, Nutsubidze, p. 150, pl. 35, fig. 1

1994 *Erycites exulatus* sp. nov., Callomon & Chandler, p. 22, pl. 1, fig. 1-2, pl. 2, fig. fig. 1-2

1994 *Erycites* aff. *exulatus* sp. nov., Callomon & Chandler, p. 23, pl. 1, fig. 4

1996 *Erycites barodiscus* Gemmellaro, Rulleau, p. 6, pl. 25, fig. 1-2, 3-4

1997 *Erycites barodiscus* Gemmellaro, Cresta, p. 42, p. 43, fig. 12, p. 44, fig. 13/F, pl. 3, fig. 1, 2, 5

2001 *Erycites barodiscus* GEMMELLARO, RULLEAU et al., pl. 27, fig. 6

2002 Erycites barodiscus GEMMELLARO, CRESTA, p. 196-197, fig. 129

2005 *Erycites barodiscus* GEMMELLARO, PALLINI et al., p. 17, pl. 9, fig. 2, 4, pl. 16, fig. 7

2008 Erycites barodiscus GEMMELLARO, IPPOLITOV et al., p. 46, fig. 1

Material: 18 internal casts of different state of preservation

# Dimensions

Dimensions										
specimen	D	Н	h	W	W	U	u			
ETA11A	126	36	28%	34	94%	58	46%			

specimen	D	Н	h	W	w	U	u
EP69A	124	31	25%	30	97%	65	52%
EG19	114	37	32%	32	86%	45	40%
ETA5	108	34	31%	32	94%	56	52%
ETA10	88	28	32%	26	93%	38	43%

#### Description

Medium-sized form with moderately evolute coiling. The umbilicus is narrow and deep on the inner whorls, becoming wider and shallower on the last whorl. The umbilical walls are strikingly convex on the phragmocone and more flattened on the body chamber without umbilical margin. The flanks of the inner whorls are considerably convex, becoming moderately rounded on the last whorl. No ventrolateral edge is present. The venter is broad, low and convex with a narrow, smooth band in the middle. The whorl-section is either depressed subcircular or wide-oval on the phragmocone, and wide-oval on the body chamber with maximum width at the mid-flank. The last whorl is always wider than the penultimate one. The length of the body chamber is about 3/4 of a whorl. The projected, oblique peristome is followed by a wide, deep and also oblique constriction. The ornamentation consists of coarse ribbing persisting throughout the shell. Thick, slightly prorsiradiate primary ribs emerge on the umbilical wall branching into 2-3 secondaries at mid-height. The primaries become prorsiradiate and widely spaced on the body chamber with concave interspace. The example EG19 bears 27 primary ribs on the last whorl. The secondaries are covered by the whorls on the phragmocone. The thinner secondary ribs bend gently forward and die out in the middle of the ventral part, alternating on the two sides. Intercalatories rarely appear on the body chamber. The suture-line is characterised by erycitid structure: the E is short with length 1/3 of the long, broad and ramified L, the U lobe is divided and strongly oblique (Figure 10).



Figure 10. Suture-line of *E. barodiscus* GEMMELLARO (ETA11A)

Remarks

In 1886 GEMMELLARO introduced two taxa, Hammatoceras (Erycites) sutneri and H. (Erycites) barodiscus, however, without figures and indication of the exact stratigraphic range (1886:205-206). None of them was later cited in the literature. Owing to these insufficiencies, a new species, Erycites exulatus sp. nov. was proposed by Callomon & Chandler (1994:22) based on a strikingly similar form from Dorset. Having made a detailed revision of the Gemmellaro-collection, Erycites exulatus was still considered as a junior synonymy of E. barodiscus, consequently its validity was rejected by CRESTA (1997). The author designated the lectotypes of both Gemmellaro species, and first figured the specimens (l.c.). After CRESTA's paper the original taxon names have been commonly accepted (RULLEAU, 1996, RULLEAU ET AL., 2001, CRESTA, 2002, COX & SUMBLER, 2002, PALLINI et al., 2005).

A robust specimen of E. fallax BENECKE was figured by Nutsubidze from the Caucasus (1966, pl. 35, fig. 1). It significantly differs from the other presented E. fallax (pl. 33, fig. 4), which seems to agree well with the holotype of E. fallifax. The diameter (D: 106) of the first example is larger than the typical size of E. fallifax (D<100), moreover the ratio of the last whorl is very close to that of E. barodiscus (H: 27, W: 33 [corrected by us!]), as the body chamber is wider than the phragmocone. By reason of the sculpture and the style of coiling, in the present study it is considered that the presence of E. barodiscus in can be documented by Caucasus NUTSUBIDZE's Erycites example figured on pl. 35, fig. 1.

#### **Comparisons**

The specific morphological features of most Gerecse specimens are well consistent with those of the lectotype designated by CRESTA (1997, p. 43, fig. 12), however, some of them show intraspecific variability. The last whorl of the example EP69 is as wide as the penultimate, while the example EG19 (Pl. 10, fig. 1) with a moderately involute coiling and thinner, radiate, well-defined primaries resembles the *E. gonionotus* figured by ROMAN (1935, pl. 1, fig 8).

The cadicone inner whorls of *E. barodiscus* and *E. fallifax* are similar, however, the two taxa differ in other characteristics. *E. barodiscus* is a more robust form with larger size (adult D>100), and with the body chamber being always wider than the phragmocone. Furthermore, *E. fallifax* is less strongly ribbed on the body chamber. *E. sutneri* differs from *E. barodiscus* by having

slightly more involute coiling and narrower, highoval whorl-section with less developed ornamentation. *Cagliceras elaphum* is also a similar form in size, but it is characterised by narrower whorls and a high-oval section, and it bears shorter primary and finer secondary ribs.

#### Distribution

Italy – Monte Erice: Lower Aalenian (CRESTA, 1997:43), Apennines: Toarcian – Aalenian boundary (CRESTA, 2002:197)

Great-Britain – Burton Cliff, Dorset: Scissum Zone (CALLOMON & CHANDLER, 1994:23, CALLOMON & COPE, 1995:67, COX & SUMBLER, 2002:37)

Georgia – North Caucasus: Lower Aalenian (NUTSUBIDZE, 1966:151)

Ukraine – Crimea: Aalensis Zone (IPPOLITOV et al., 2008:43)

France – La Verpillière, Veyras: Upper Lias (DUMORTIER, 1867:267), Veyras: Murchisonae Zone (ROMAN, 1935), Belmont: Aalensis Zone (RULLEAU, 1996, pl. 25), Saint-Quentin: Lugdunensis Subzone or Opalinum Zone (RULLEAU et al., 2001, pl. 27)

Hungary – Gerecse Mts: Meneghinii to Opalinum Zones

1966 Erycites subquadratus n. sp., GÉCZY, p. 95, p. 96, fig. 81, pl. 27, fig. 1-2, pl. 42, fig. 1-2
1968 Erycites subquadratus GÉCZY, GÉCZY, p. 127, pl. 3
1996 Erycites aff. subquadratus GÉCZY, RULLEAU, p. 6, pl. 26, fig, 1-2

Material: 2 internal moulds of moderate preservation

Dimensions

specimen	D	Н	h	W	W	U	u
ETA11B	115	31	27%	32	103%	56	49%
EG25	114	31	27%	31	100%	56	49%

# Description

Medium-sized form with evolute coiling and an umbilicus growing gradually wider. The umbilical wall is steep and convex on the phragmocone, becoming less convex on the last whorl. The flanks are convex on the inner whorls, but become flattened on the body chamber with a rounded ventrolateral shoulder. The venter is broad, low and slightly convex bearing a ventral smooth band. The cross-section of the inner whorls is wide-oval, but it becomes subquadrangular on the last coiling. The maximum thickness of the section lies a little below the midflank. The last whorl bearing a body chamber of

3/4 whorl length is wider than the penultimate. There is a deep and oblique constriction behind the projected peristome. The ribbing persists to the peristome, and consists of well-developed, radial primary ribs that branch into 2 or 3 secondaries. The primaries become prorsiradiate and widely spaced on the body chamber. The example ETA11B bears about 26 primaries on the last whorl. The thinner secondary ribs curve moderately forward, and reach the intersection alternating on the two sides. The suture structure is erycitid with short E, long and ramified L, divided and oblique U.

# Remarks and comparisons

Erycites subquadratus n. sp. was created on the ground of 8 specimens by GÉCZY in 1966. It shows striking similarities to the lectotype of E. barodiscus figured by CRESTA (1997). Having revised the Csernye and the Gerecse materials, E. subquadratus and E. barodiscus appear closely allied species, although not identical. Both taxa have some common morphological features (e.g. size, style of coiling, sculpture, suture-line), but E. subquadratus differs from E. barodiscus in at least a major specific characteristic. The latter bears convex flanks on the body chamber with wideoval whorl-section, while the section of E. subquadratus is markedly subquadrangular. This difference already emphasized by RULLEAU (1996) is a specific one, therefore the validity of E. subquadratus seems to be well-established.

The *E. barodiscus* and the *E. subquadratus* examples documented from France by RULLEAU (1996, pl. 25, fig. 1-4, pl. 26, fig. 1-2) slightly differ from the types by possessing broader whorls.

#### Distribution

France – Belmont: Aalensis Zone (RULLEAU, 1996)

Spain – Erycites sp. cf. E. subquadratus GECZY: Zegri Sur: Lower Aalenian (LINARES & RIVAS, 1971:192), Cerro Méndez 2. sect.: Opalinum Subzone (GARCIA-GÓMEZ et al., 1994:216), E. aff. subquadratus GECZY: Coll de Port: Opalinum Zone (FAURE & ALMERAS, 2006:650)

Portugal – *Cagliceras* aff. *subquadratum* (GÉCZY): Sao Giao: Reynesi Subzone (ELMI et al., 2007:120)

Hungary – Csernye: Upper Toarcian, Gerecse Mts: Aalensis and Opalinum Zones

Erycites gerecsensis n. sp. (Pl. 12, fig. 1-2)

Holotype: EG31A

Derivation of name: The name refers to the type locality.

Type locality and horizon: Kis-Gerecse quarry near Süttő, Gerecse Mts, bed 31, Aalensis Zone

Material: a single well-preserved internal mould

#### Dimensions

specimen	D	Н	h	W	W	ح	u
EG31A	110	32	29%	28	87%	53	48%

#### Diagnosis

Erycitid coiling, wide and shallow umbilicus. Venter broad and rounded with smooth band. Whorl-section wide-oval on the phragmocone, oval-shaped on the body chamber. Coarse, trifurcating ribbing with tubercles at the furcation points on the last whorl. Erycitid suture-line structure.

#### Description

Medium-sized, moderately evolute shell, with a robust, erycitid coiling. The umbilicus is narrow and deep on the inner whorls, while shallow and wide from the penultimate whorl. The flanks are convex on the phragmocone, becoming less rounded on the body chamber. Neither umbilical, nor ventrolateral edges are present. The ventral part is broad and convex with a narrow, smooth band in the middle. The cross-section is wide-oval on the inner whorls, while oval-shaped on the body chamber. The last whorl is as wide as the penultimate. The length of the body chamber is 3/4 of a whorl. The ribbing persists on the entire shell and consists of well-defined, thick and radiate primaries that emerge on the umbilical wall and trifurcate at the lower third of the flank. The primary ribs develop into projected, elongated tubercles with concave intercosta on the body chamber. The example bears 19 widely spaced primaries on the last whorl. Intercalatory ribs appear irregularly between the secondaries that curve forward on the venter, and alternately fade away in the middle. The aperture is missing, but the wide, deep and prorsiradiate constriction behind the peristome is preserved. The suture-line is the same as that of *E. barodiscus*.

#### Remarks

The example figured here seems to be close to the lectotype of *E. barodiscus* (in CRESTA, 1997:43, fig. 12) in its size and suture-line structure, but it markedly differs in the style of coiling and the ornamentation. The body chamber of *E. barodiscus* is always wider than the penultimate whorl, and the cross-section is slightly depressed wide-oval. On the other hand, the

section of the body chamber of *E. gerecsensis* n. sp. is higher oval-shaped, because the last whorl is not wider than the penultimate. Furthermore, the example is more rarely ribbed with radial, tubercular primaries branching at the lower third, which is not typical of *E. barodiscus* (see CRESTA, 1997:42). The specimen resembles the *E. barodiscus* figured by RULLEAU (1996, pl. 25, fig. 1-2), which also bears nodular primaries, however, trifurcating at the mid-hight of the flank.

E. barodiscus, E. subquadratus and E. gerecsensis n. sp. all possess more robust and larger shell than that of the usual erycitid forms. Considering the morphology and the stratigraphic range, the three taxa appear closely allied species.

#### Distribution

The specimen comes from the Aalensis Zone (bed 31, Kis-Gereese section). It is associated with *Dumortieria stricta, Cagliceras rotundiformis* and *Erycites ovatus*.

# Erycites intermedius HANTKEN in PRINZ, 1904 (Pl. 13, fig. 1, 5)

- 1904 Erycites Schafarziki nov. sp., PRINZ, p. 93, pl. 17, fig. 2
- 1904 Erycites intermedius nov. sp. Hantken msc., Prinz, p. 94, pl. 16, fig. 1, pl. 38, fig. 3
- 1921 Erycites partschi Prinz, Buckman, Vol. III, pl. 246, fig. 1
- 1925 Erycites intermedius HANTKEN und PRINZ, 1904, RENZ, p. 195, pl. 3, fig. 4
- 1966 Erycites intermedius HANTKEN in PRINZ, 1904, GÉCZY, p. 92-94, fig. 78-79, pl. 25, fig. 1, 4, pl. 26, fig. 1, pl. 41, fig. 13-15
- 1968 Erycites intermedius HANTKEN in PRINZ, 1904, PINNA, p. 26, pl.3, fig.3, pl.2 n.t., fig.18
- 1978 Erycites intermedius HANTKEN in PRINZ, 1904, DEZI & RIDOLFI, p. 54, fig. 79-80
- 2001 Erycites (Erycites) intermedius HANTKEN in PRINZ, 1904, RULLEAU et al., pl. 27, fig. 5
- 2008 Erycites intermedius HANTKEN in PRINZ, 1904, MARIOTTI et al., p. 6, fig. 5/a

Material: 6 poorly preserved and 3 relatively well-preserved internal casts

#### Dimensions

specimen	D	Н	h	W	W	U	u
ETB32	122	36	30%	26	72%	51	42%
ETB30B	92	28	30%	?		42	45%

#### Description

Medium-sized, moderately evolute form with a wide, gradually deepening umbilicus. The umbilical wall is low and gently convex, both the umbilical and the ventrolateral margins are

rounded. The flanks are slightly convex. The ventral part is low and broad on the phragmocone, becoming a little higher and narrower on the body chamber. The venter is divided by a smooth band in the middle. The whorl-section of the inner whorls is wide-oval growing highly arched on the last whorl with maximum width at the lower third. No whole body chambers are preserved. The ornamentation is characterised by a regular, coarse ribbing. The primary ribs emerging on the umbilical wall are straight and prorsiradiate. Their intercostal spaces are gently wider than the ribthickness. The primaries are rursiradiate and also more widely spaced on the body chamber. The primary ribs trifurcate at the mid-flank. The less developed secondaries are straight prorsiradiate on the phragmocone, becoming curved forward on the last whorl. Alternating on the two sides, they fade away in the middle of the venter. The example ETB32 bears 33 primaries on the last whorl. Due to the corroded surfaces the suture-lines are not visible in all details, but the specific erycitid configurations can be traced. The length of the E lobe is half of the broad L. The saddles being less developed resemble that of E. fallifax, U2 and U3 are markedly oblique.

#### Remarks and comparison

From the Upper Aalenian sequences of the Bakony Mts three new *Erycites* species with resembling morphology were introduced by PRINZ (1904: 83-85): *E. Partschi* nov. sp., *Erycites Schafarziki* nov. sp., *E. intermedius* nov. sp. Hantk. msc.. *E. schafarziki* PRINZ was reclassified as *E. intermedius* by GÉCZY (1966:93) on the ground of the identical sizes, shapes, sculptures and suture-lines of the two holotypes (see PRINZ, 1904, pl.17, fig.2 refigured by GÉCZY, 1966, pl. 26, fig. 1).

The Gerecse examples show close agreement with the holotype (GÉCZY, 1966: pl. 25, fig. 4).

Cagliceras elaphum is one of the nearest forms to E. intermedius. DONOVAN (1958:58) drew particular attention to the striking similarities of the two taxa in morphology. However, GÉCZY (1966: 93, 97) and PINNA (1968:26) gave a detailed description of the specific features making distinguishable the taxa, respectively. The validity of E. intermedius was again confirmed by DEZI & RIDOLFI (1978:54), GOY et al. (1995:103), RULLEAU et al. (2001, pl. 27, fig. 5), and the revision of the Gerecse material has yielded the same results. The major morphological differences can be observed in the coiling style, in the sculpture and the suture-line. C. elaphum is characterised by a more evolute shell (H/D of C. elaphum: 23-26%, H/D of E. intermedius: 30-32%), as well as short and thick, almost tubercled primary ribs that branch on the lower third, while primaries of E. intermedius are longer, furcating at the middle of the flanks. Proportion of E and L lobes is 1/3 on C. elaphum, while it is 1/2 on E. intermedius, and the lateral saddle on the latter is less developed. E. partschi PRINZ is another close form to E. intermedius, however, it differs in the coiling style, the whorl-section and the ornamentation. E. partschi has a somewhat more evolute shell with narrower whorl, shallow umbilicus, flattened flank, and sharp umbilical edge. Furthermore, it is densely and finely ribbed with weakly developed umbilical tubercles (PRINZ, 1904:83). One of the Gerecse examples, ETB30A gently resembles E. partschi, it might be a transitional form. Its sculpture style is like that of E. intermedius, but it bears a steep, flat, disornamented umbilical wall with margin only on the body chamber.

#### Distribution

Italy – Monti Martani: Toarcian (PINNA, 1968:26), Gorgo a Cerbara: Murchisonae Zone (Haugi Subzone) (KÄLIN & URETA, 1987:505), Monte Catria and M. Nerone: Fallifax and Klimakomphalum Biozones (CRESTA, 1994:115), Caloveto: Opalinum Zone (MARIOTTI et al., 2008:5), E. schafarziki: Aalenian (RENZ, 1923:268)

Greece – Kap, EPIRUS: Opalinum – Murchisonae Zones (RENZ, 1910:598), Korfu: Lower Dogger (RENZ, 1910:587, 1925:195)

Austria – Nordtirol: Murchisonae Zone (FISCHER, 1969:106)

France – La Verpillière: Opalinum Zone (RULLEAU et al., 2001: pl. 27, fig. 5)

Great Britain – Horn Park Quarry, Dorset: Bradfordensis Subzone (BUCKMAN, 1921: pl. 246), Murchisonae Zone (CALLOMON & CHANDLER, 1990:94, COX & SUMBLER, 2002:50)

Hungary – Csernye: Upper Aalenian (GÉCZY, 1966:94), Gerecse Mts: Opalinum and Murchisonae Zones

# Erycites sp. aff. reussi (HAUER, 1856) (Pl. 13, fig. 3-4)

1856 Ammonites Reussi, Hauer, p. 50, pl. 20, fig. 1-3 1904 Erycites reussi Hauer, Prinz, p. 85

- ? 1915 Hammatoceras Reussi (HAUER), PRINCIPI, p. 446 1934 Erycites cfr. Reussi HAUER, MERLA, p. 23, pl. 2,
- ? 1960 Erycites cf. reussi HAUER, LELIEVRE, p. 36, pl. 7, fig. 1
  - 1963 Erycites reussi (HAUER), KOTTEK, p. 126
  - 1966 *Erycites reussi* (HAUER), GECZY, p. 100, fig. 86, pl. 28, fig. 5, pl. 42, fig. 6

1978 Erycites cfr. reussi (HAUER), DEZI & RIDOLFI, p. 56, fig. 83-84

Material: a single well-preserved internal mould

#### Dimensions

specimen	D	Н	h	W	W	U	u
EG6	68	24	35%	30	125%	27	40%

#### Description

Medium-sized form with moderately evolute coiling and gradually growing whorls. The umbilicus is deep and slightly wide, the umbilical wall is low and rounded. Neither umbilical nor ventrolateral margin is characteristic. The flanks are significantly convex. The venter is low and broadly rounded, with a weakly developed carina. The whorls are depressed (H/W: 80%), the maximum width lies a little below the mid-height. No body chamber is preserved. The ornamentation consists of moderately strong ribbing. The radiate primary ribs rising from the umbilical wall bifurcate at the upper third of the flank. There are 25 primaries on the last whorl. The thinner secondary ribs are first rectiradiate, then bend slightly forward, and reaching the keel fade away. Intercalatories appear on the upper third of the flank. The suture-line is characterised by a short E, a gently asymmetrical, long and ramified L, and well-developed and oblique U2, U3. The high accessory saddle somewhat differs from that of the typical erycitid lobe structure (Figure 11).



Figure 11. Suture-line of *E.* sp. aff. *reussi* (HAUER) (EG6)

#### Remarks and comparisons

Regarding the morphology and the suture construction the Gerecse example is close to the type (HAUER, 1856:50, pl. 20, fig. 1-3), but slight differences are observable in the ribbing and the whorl-section.

The similar taxa clearly differ in morphology from *E. reussi*. Having narrower whorls, the cross-section of *E. baconicus* is subcircular, while it is

subquadrangular on *E. barodiscus*, which, otherwise, has prorsiradiate ribbing. *E. reussi* was compared to *E. rotundiformis* by MERLA (1934:24). Accordingly, the latter is more finely ribbed, and its section is never depressed. The *Erycites (Erycites)* aff. *sphaeroconicus* figured by RULLEAU et al. (2001, pl. 28, fig.2) resembles *E. reussi* in the coiling style and the sculpture, but it differs from the latter by having less depressed cross-section.

#### Distribution

Austria – Königsbach, Adneth, Thurnberg, Hochleitengraben, Ammergau (HAUER, 1856:60)

Italy – Monti Martani, M. Subasio: Upper Lias (PRINCIPI, 1915:447), Montagna della Rossa, Cagli: Jurense Zone (MERLA, 1934:24), Alpe Turati: Upper Toarcian (VENZO, 1952:116)

Greece – Epirus: Upper Lias (RENZ, 1910:566), Argolis: Lower Dogger (KOTTEK, 1963:126)

?Morocco – Krendegg: Bradfordensis Subzone (LELIÈVRE, 1960:37)

Hungary – Csernye: Toarcian Stage (GÉCZY, 1966:101), Gerecse Mts: lower Murchisonae Zone

# Erycites fallifax ARKELL, 1958 (Pl. 11, fig. 1, 2)

- 1865 Ammonites fallax, BENECKE, p. 171, pl. 6, fig. 1-3 1886 Hammatoceras fallax BENECKE, VACEK, p. 93, pl. 15, fig. 1-9
- 1904 Erycites fallax Benecke, Prinz, p. 89, pl. 25, fig. 1 1923 Erycites fallax Benecke, Roman & Boyer, p. 31, fig. 23, pl. 6, fig. 1
- 1934 Erycites fallax (BENECKE), MERLA, p. 28
- 1935 Erycites fallax BENECKE, ROMAN, p. 15, pl. 1, fig. 7
- 1957 Erycites fallifax, ARKELL, p. L267, fig.308.3
- 1966 *Erycites fallifax fallifax* ARKELL GÉCZY, p. 106-109, pl. 30, fig. 2, 4, pl. 31, fig. 1, pl. 43, fig. 1
- 1966 *Hammatoceras (Erycites) fallax* BENECKE, NUTSUBIDZE, p. 151, pl. 33, fig. 4
- 1976 Erycites cf. fallifax Arkell, Braun & Jordan, p. 27, p. 28, fig. 5, pl. 3, fig. 8
- 1988 Erycites fallifax Arkell, Linares et al., pl.1, fig. 8
- 1990 Erycites fallifax ARKELL, CECCA et al., pl. 2, fig. 2
- 1993 Erycites fallifax Arkell, Elmi & Rulleau, pl. 2, fig. 3-4
- 1994 Erycites fallifax ARKELL, GARCIA-GÓMEZ et al., pl. 1, fig. 13
- 1994 Erycites cf. fallifax Arkell, Callomon & Chandler, p. 21-22, pl. 1, fig. 1-3
- 1996 Erycites fallifax Arkell, Rulleau, p. 11, pl. 37, fig. 1-2
- 1997 Erycites fallifax Arkell, Cresta, p. 44, fig. 13/H
- 1997 Erycites fallifax ARKELL, CASSEL, pl. 8, fig. 1
- 2000 Erycites fallifax Arkell, Henriques, pl. 1, fig. 1

2005 Erycites fallifax ARKELL, PALLINI et al., p. 17, pl. 9, fig. 1

Material: 9 internal casts of different state of preservation, and 3 fragments

#### Dimensions

specimen	D	Н	h	W	w	U	u
ETA4	92	21	23%	20	95%	49	53%
EP61	90	25	27%	22	88%	43	48%

#### Description

Medium-sized, erycitid form with sphaerocone inner coiling. The umbilicus is narrow and deep on the phragmocone, becoming wider on the body chamber. The umbilical wall is steep and convex on the inner whorls, and less rounded on the last whorl. The flanks are convex on the phragmocone, becoming slightly flattened on the body chamber. The venter of the last whorl is narrow, high and rounded without ventral keel. The cross-section of the inner whorl is wide-oval, while it is high-oval on the body chamber with maximum thickness at the lower third of the flank. The last whorl, being more compressed, is as wide as the penultimate, or a little narrower than that. The length of the body chamber is 4/5 of a whorl. The moderately projected peristome is prorsiradiate with a shallow constriction behind. The ornamentation is characterised by a weakly developed ribbing. Thin primary ribs rise from the umbilicus, their interspace are wider than the rib-width on the inner coiling. The primary ribs branch into 2 or 3 secondaries at the mid-flank. The secondaries are covered on the phragmocone. The primaries grow stronger and are straight and prorsiradiate on the body chamber. The example ETA4 bears 26 primaries on the last whorl. The less developed and prorsiradiate secondaries fade away in the middle of the ventral part. The suture-line shows a slightly simpler erycitid character. The length of E is half of the broad L. The lateral saddles are widely divided by U2. The U lobes are oblique (Fig. 12).



Fig. 12. Suture-line of *E. fallifax* ARKELL (ETA4)

#### Remarks and comparisons

As type species had not been designated by BENECKE, it was done by ARKELL (1957:267, fig.308.3) designating BENECKE's (BENECKE, 1865, pl. 6) as the holotype of E. fallifax. According to CALLOMON & CHANDLER (1994:22), the size of the holotype is smaller than the average taxon size. Moreover, E. fallifax appears to show intraspecific variabilities, consequently, there are significant differences in the size, the coiling style, the section and the sculpture between the specimens figured in the literature. GÉCZY (1966: 106-112) made an attempt at solving this problem on the basis of the Csernye erycitid material containing 88 wellpreserved, adult E. fallifax specimens. The author reclassified the taxon introducing four new subspecies: E. fallifax fallifax Arkell, 1957, E. fallifax excavatus n. subsp., E. fallifax flexuosus n. subsp., E. fallifax arkelli n. subsp., however, this classification has not been accepted in the literature

The Gerecse sample is also characterised by intraspecific variabilities. While the examples EP61 and ETB39 agree well with the holotype, the examples ETA4 and ETAF1 differ from that in morphology. The latter two are larger forms with less sphaerocone inner coiling, less convex flanks on the body chamber and more prorsiradiate ribbing. The two specimens are close in morphology to *E. fallifax excavatus* GÉCZY, but they bear more widely spaced ribbing, and less developed keel. The fragmentary ETB29A is also similar to the latter subspecies by having narrower whorls and less convex flanks, but differs in the sculpture as well.

#### Distribution

E. fallifax is typical of the Opalinum and Murchisonae Zones of Europe (Italy, Spain, Portugal, France, Great Britain, Germany, Greece - Géczy, 1966:108, Callomon & Chandler, 1994:21, PALLINI et al., 2005:17), as well as it is known from North Africa (ELMI, 1986:233, 1996:127), from the SADKI, Caucasus (KRYMHOLZ, 1961, NUTSUBIDZE, 1966), Thailand (BRAUN & JORDAN, 1976), North America and Zealand (WESTERMANN, WESTERMANN et al., 2000, HUDSON, 2003). In Hungary the species has been documented from the Aalenian of Csernye (GÉCZY, 1966:108), and it is typical of the Opalinum and Murchisonae Zones of the Gerecse assemblage.

# Subgenus Abbasitoides GECZY, 1966

Type species: Coeloceras modestum VACEK, 1886

The type species (VACEK, 1886, p. 100, pl. 17, fig. 4-6) was designated by GÉCZY (1966:115).

#### Diagnosis

Small-sized, subserpenticone form with gradually growing coiling and wide umbilicus. The whorl-section is subcircular, the ribbing is weakly developed without tubercles. No keel is present, the venter is divided by a smooth band. Erycitid suture-line with short E, long, ramified L, divided, oblique U.

#### Remarks

The last period of the phylogeny of Erycitinae is characterised by the gradually reduced size of the shell. *Malladaites, Abbasites, Ambersites* and *Abbasitoides* are all small-sized forms. Only the latter taxon can be investigated from the Hungarian erycitid materials, furthermore, comparing to the Csernye sample (29 specimens), the occurrence of *Abbasitoides* (2) has not been considerable in the Gerecse assemblage.

The close resemblance of *C. modestum* and the Erycites group was already emphasized by VACEK (1886:100) and PRINZ (1904:100), and both authors regarded the former taxon as the direct ancestor of the stephanoceratids. The species was classified later within Docidoceras by ARKELL (1956:177) and LELIÈVRE (1960:47). The erycitid character of the suture-line, as well as the phylogenetic importance of C. modestum was underlined by WESTERMANN (1964). Based on the suture construction and the ventral interruption of the ribbing, GÉCZY (1966:115) distinguished the from the genera Coeloceras Docidoceras, and placed it into Erycites. Moreover, having created the new subgenus Abbasitoides. **GÉCZY** regarded as it taxonomically independent **Erycites** group: (Abbasitoides) modestus (VACEK), (Abbasitoides) modestus crassornatus n. subsp., E. (Abbasitoides) modestus compressus (PRINZ).

The morphological similarity of *A. modestus* and *Docidoceras planulatum* BUCKMAN was also noted by GÉCZY, however, without reclassification of the latter. (The taxonomic position of *D. planulatum* has been recently discussed by CHANDLER & DIETZE (2004:223). Accordingly, *Mollistephanus planulatus* (BUCKMAN) appears to be a connection form between *Riccardiceras* and *Mollistephanus* as the earliest representative of the latter genus.)

#### Distribution

The subgenus is known from the Aalenian of Europe and North Africa.

# Abbasitoides modestus (VACEK, 1886) (Pl. 9, fig. 2-3, Pl. 13, fig. 2)

- 1886 Coeloceras modestum n. sp., VACEK, p. 100, pl. 17, fig. 4-6
- 1904 Coeloceras modestum VACEK, PRINZ, P. 100, PL.25, FIG. 3
- 1923 Coeloceras modestum Vacek, Renz, pl. 12, fig. 10 1964 Erycites (n. subgen.?) modestus (Vacek), Westermann, pl. 6, fig. 8
- 1966 Erycites (Abbasitoides) modestus (VACEK, 1886), GÉCZY, p. 116-117, fig. 102, pl. 33, fig. 1, pl. 44, fig. 5
- 1970 Erycites (Abbasitoides) modestus (VACEK), FISCHER, p. 602, pl. 4, fig. 7
- 1988 Abbasitoides modestum (VAC.), LINARES et al., pl. 2, fig. 4
- 1990 Stephanoceras (Abbasitoides) modestum (VACEK), CALLOMON & CHANDLER, pl. 1, fig. 2
- 1990 Stephanoceras (Abbasitoides) aff. modestum (VACEK), CALLOMON & CHANDLER, pl. 1, fig. 3-4
- 1995 *Abbasitoides modestus* (VACEK), WESTERMANN, p. 114, pl. 17, fig. 4
- 2001 Erycites (Abbasitoides) modestus (VACEK), RULLEAU et al., pl. 29, fig.3-4

Material: two poorly preserved internal moulds *Dimensions* 

specimen	D	Н	h	W	W	U	u
ETB30B	43	14	32%	14	100%	21	49%
ETA7	35	12	34%	12	100%	14	40%

#### Description

Small-sized, subserpenticone form with a wide and shallow umbilicus. The coiling is gradually grown, the last whorl is wider than the penultimate. The flanks are convex without umbilical and ventrolateral margins. The venter is broad and rounded, the whorl-section is subcircular with maximum width at the midheight. The ornamentation consists of fine ribbing, which persists throughout the whorls. The primaries emerging from the umbilicus bifurcate at the mid-flank. The secondaries that first bend slightly backward, curve forward on the venter, and fade away in the middle. They alternate with a narrow smooth band between them. The example ETB30 bears 32 ribs on the outer part of the last half whorl. Although the body chamber of the latter specimen is preserved, its exact length cannot be observed due to the corroded surface. The simple peristome is slightly projected, without constriction. Due to the state of preservation, the suture-line is not visible.

#### Remarks and comparison

The classification of the species has been controversial. The taxon was regarded as belonging to *Stephanoceras*, as the microconch of

"Stephanoceras" (M) longalvum (VACEK) by CALLOMON & CHANDLER (1990). It was also considered as the earliest representative of the Otoitidae as Stephanoceras (Abbasitoides) modestum by PAGE (1993:217). As opposed to this, based on the suture-line structure, the ventral interruption and the simple aperture, WESTERMANN (1964, 1995) has always regarded A. modestus as a small-sized erycitid macroconch.

Both Gerecse specimens, as well as the Csernye material are slightly larger than the holotype (VACEK, 1886:100, pl. 17, fig. 4-6). The example ETB30B (Pl. 9, fig. 2-3) being a more evolute form resembles the Csernye sample and the specimen figured by CALLOMON & CHANDLER (1990, pl. 1, fig. 3), while the example ETA7 (Pl. 13, fig. 2) having narrower umbilicus is closer to the type and the specimens figured by RULLEAU et al. (2001, pl. 29, fig. 3-4) and CALLOMON & CHANDLER (1990, pl. 1, fig. 2).

#### Distribution

Italy – Cap San Vigilio: Lower Dogger (VACEK, 1886:100), Valdorbia: Murchisonae Zone (BONARELLI, 1893), Fonte Caldarense, Cesi, Terni: Lower Dogger (RENZ, 1923:268), Gorgo a Cerbara: Murchisonae Zone (Haugi Subzone) (KÄLIN & URETA, 1987:505) Monte Nerone: Murchisonae Zone (CECCA et al., 1990, CRESTA, 1996), Fallifax Biozone (CRESTA, 1994:115), Opalinum – Murchisonae Zones (CALLOMON et al., 1995), Colle d'Orlando: Murchisonae Zone (Parisi et al., 1998:23), Mt. Magaggiaro: Lower Aalenian (PALLINI et al., 2005)

Spain – Cordilleras Béticas: Comptum Subzone – Concavum Subzone (Linares et al., 1988, Henriques et al., 1996:145), Cuenca Ibérica: Murchisonae Biozone (Fernández-López & Gómez, 1990:75), Sierra de San Pedro: Murchisonae Zone (Linares & Sandoval, 1992:96), Sierra de Ricote: Comptum Subzone – Murchisonae Zone (Garcia-Gómez et al., 1994:213), Cerro Méndez 2. sect.: Comptum Subzone – Murchisonae Zone (Garcia-Gómez et al., 1994:216), Zegri Norte: Opalinum – Murchisonae Zones (Garcia-Gómez et al., 1994:217), Llaberia: Aalenian (Fernández-López et al., 1998:215)

Austria – Nordtirol, Scheibelberg II: Murchisonae Zone (FISCHER, 1970:602)

Portugal – North Lusitanian Basin: Bradfordensis Subzone (HENRIQUES, 1995:231)

Greece – Leukas (Anavrysada) (RENZ, 1906:753)

Great Britain – Chideock: Murchisonae Zone and Subzone, Horn Park: Concavum Zone and Subzone, Formosum Subzone (CALLOMON & CHANDLER, 1990)

France – La Roche, La Verpillière: Bradfordensis Subzone (RULLEAU et al., 2001)

Morocco – Krendegg: Murchisonae Zone (LELIEVRE, 1960:47), Almou-Abtouri: Murchisonae Zone (DUBAR et al., 1971:402),

Haut-Atlas Central: Concavum Zone (SADKI, 1996:127)

Hungary – Csernye: Upper Aalenian (GECZY, 1966:117), Gerecse Mts: Opalinum and Murchisonae Zones

# Evaluation of the Erycitinae of the Gerecse fauna

246 specimens are classified within the subfamily Erycitinae from the Gerecse assemblage. In spite of the mediocre or poor state of preservation of inner casts in the "Ammonitico Rosso marl" facies, 47% of the specimens can be identified on species level. Two genera, one subgenus, 15 species could be distinguished by 117 determined specimens.

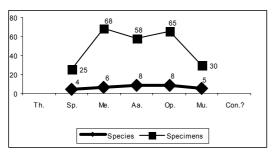


Figure 13. Change of number of the Erycitinae species and specimens (Speciosum to Murchisonae Zones)

Considering the entire fauna in the Upper Toarcian-Middle Aalenian, the erycitids form a significant part of the material from the Meneghinii to the uppermost Opalinum Zones, with a percentage of 52% in the Aalensis Zone (Figure 3). Its highest diversity can be proved from the Aalensis and Opalinum Zones with 8 species. The numbers of the erycitid species and specimens are plotted in Figure 13.

Cagliceras elaphum ranging from the uppermost Speciosum to the middle Opalinum Zones form the largest part of species with 32 specimens. Erycites ovatus and E. barodiscus also have a long range of four zones. Four taxa are restricted to only one zone: Cagliceras picenum and C. enigmaticum (Speciosum Zone), C. costulosum and E. gerecsensis n. sp. (Aalensis Zone), Erycites sp. aff. reussi (Murchisonae Zone). The ratio of the subfamily decreased in the Murchisonae Zone, only two taxa show gradual progression (E. fallifax, E. intermedius). Due to the uncertain presence of the Concavum Zone, the Erycitinae cannot be documented from the Upper Aalenian. Zonal changes of the numbers of specimens of the five most common taxa are plotted in Figure 14.

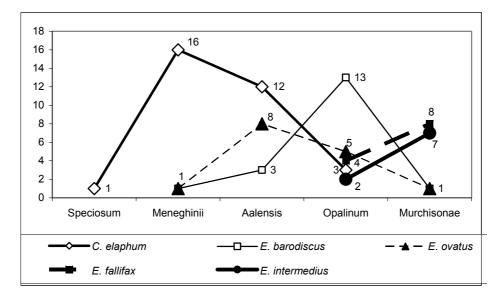


Figure 14. Numbers of *Cagliceras elaphum* (MERLA), *Erycites barodiscus* GEMMELLARO, *E. ovatus* GÉCZY, *E. fallifax* ARKELL, and *E. intermedius* HANTKEN in PRINZ (Speciosum to Murchisonae Zones) in the Gerecse sections

If the Csernye fauna is compared to that of the Gerecse Mts, it is important to underline the fact that the Csernye section is under-represented by the Middle - Upper Toarcian sequences (GÉCZY, 1966). Consequently, the 311 erycitid specimens described by GÉCZY were mainly Aalenian Erycitinae taxa. 181 specimens represent the Erycites fallifax group, while the Upper Aalenian E. intermedius (46), E. partschi (11) and specimens belonging to the subgenus Abbasitoides (29) also formed a significant part in the whole material. The diversity and number of the Upper Toarcian erycitid taxa (Erycites elaphus: 1, E. sp. cf. robustus: 1, E. sp. cf. rotundiformis: 1), and the number of species flourishing around the Toarcian-Aalenian boundary (E. subquadratus: 8, E. ovatus: 3) was markedly low. The quantitative distinction of the two faunas can be explained by the different ages of the successions, because the taxonomical and morphological affinities are strikingly close between the two assemblages, e.g. they have 9 taxa in common, and the high diversity of the subfamily in both regions is also worth mentioning. On the other hand, the proportion of the Erycitinae is closer to the data published from Italy and Portugal. The subfamily forms the highest ratio in the Ammonitina fauna from the Zone (Csernyeiceras upper Opalinum verpillierense biozone) to the lower part of the Murchisonae Zone (Abbasitoides modestus biozone) (GÉCZY, 1967:258).

The diversity of the Gerecse erycitids is in accordance with that of the Lower – Middle Aalenian succession at San Vigilio (CALLOMON et al., 1995). However, on the basis of the published data from different European Aalenian localities, the average diversity of other coeval faunas seems to be lower, 2-6 erycitid species per zone

(CALLOMON & COPE, 1995, CRESTA, 1996, HENRIQUES, 1995, 2000, PARISI et al., 1998). LINARES et al. (1988) documented 9 taxa from the Murchisonae Zone in the Betic Cordillera, more species (11) are known only from Csernye (GÉCZY, 1966). Regarding the stratigraphic distribution, as well as the change in diversity and in proportions of the subfamilies, the Gerecse material differs from those of Italy and Portugal. In the Gerecse Mts the Erycitinae reached its highest proportion in the entire fauna as early as the Aalensis Zone, and it shows a gradual decline from the Opalinum Zone, with only 14% in the Murchisonae Zone (Figure 3). In Italy, on the other hand, the subfamily forms 56% in the Opalinum Zone, and 23% in the Murchisonae Zone at Gorgo a Cerbara (see KÄLIN & URETA, 1987), its acme occurred in the Murchisonae Zone at Colle d'Orlando (PARISI et al., 1998), and it flourished in the Lower - Middle Aalenian of the Umbria Marchean Apennines (CRESTA, 1994, 1996). In Portugal, the Erycitidae is not typical of the Opalinum Zone of the North Lusitanian Basin, it appears only in the Bradfordensis Subzone (14%), reaches 28% in the Concavum Subzone and shows a decline with 15% in the Limitatum Subzone (HENRIOUES, 1995:232, and HENRIQUES et al., 1995). The abundance of the subfamily is similar at the Zambujal de Alcaria section, where it forms 4% in the Opalinum Zone, 10% in the Bradfordensis Zone and 12% in the Concavum Zone (HENRIQUES, 2000:90).

A full-scope quantitative, taxonomic and paleobiogeographic evaluation of the Upper Toarcian – Aalenian Ammonitina material of the Gerecse Mts, including other subfamilies as well, requires more revisionary research, which is in progress.

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Table 1. Distribution of Ammonitina (Thouarsense to Murchisonae Zones), Kis-Gerecse section (not all

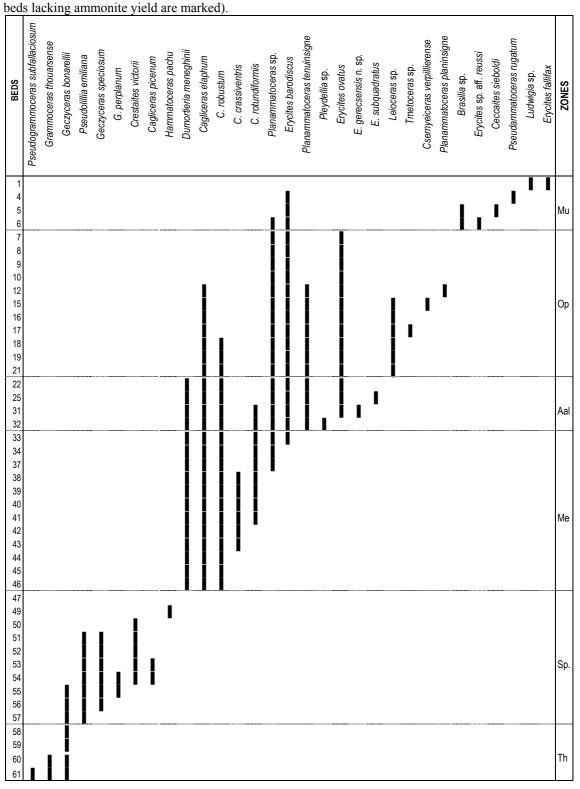
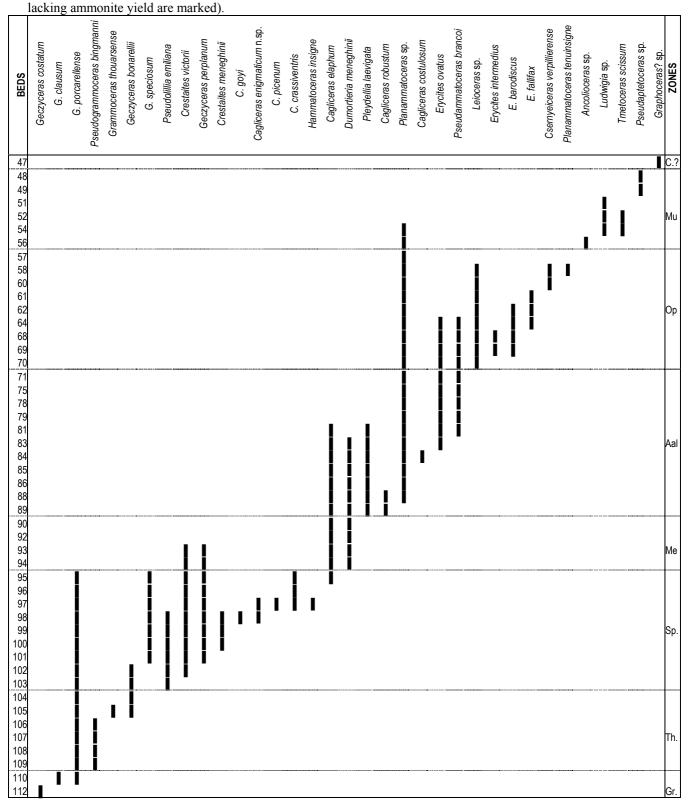


Table 2. Distribution of Ammonitina (uppermost Gradata to Murchisonae Zones), Pisznice section (not all beds



 $Table\ 3.\ Distribution\ of\ Ammonitina\ (Thouarsense\ to\ Murchisonae\ Zones),\ T\"{o}lgyh\'{a}t\ "A"\ section\ (not\ all\ Murchisonae\ Zones),\ T\~{o}lgyh\'{a}t\ "A"\ section\ (not\ all\ Murchisonae\ Zones),\ T\~{o}lgyh\'$ 

beds lacking ammonite yield are marked).

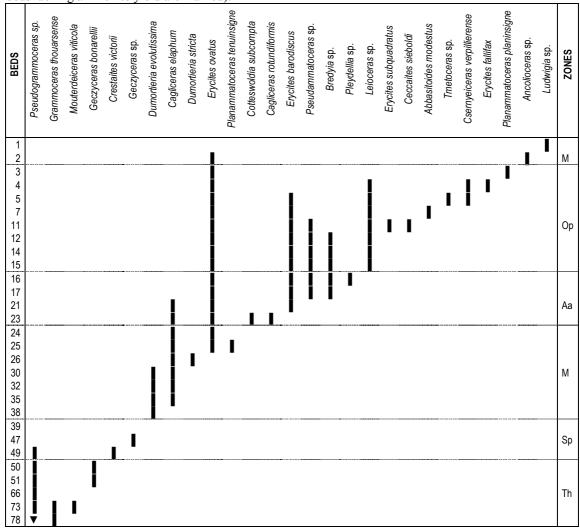
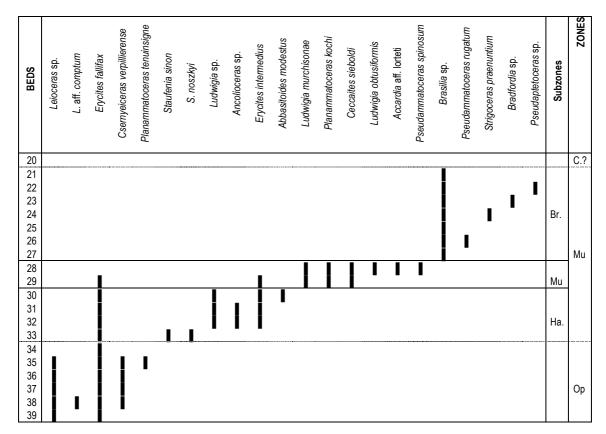


Table 4. Distribution of Ammonitina (Opalinum to Murchisonae Zones), Tölgyhát "B" section.



## **Plates**

(The specimens are coated with ammonium chloride, and are shown in natural size. The last chambers are marked by \*.)

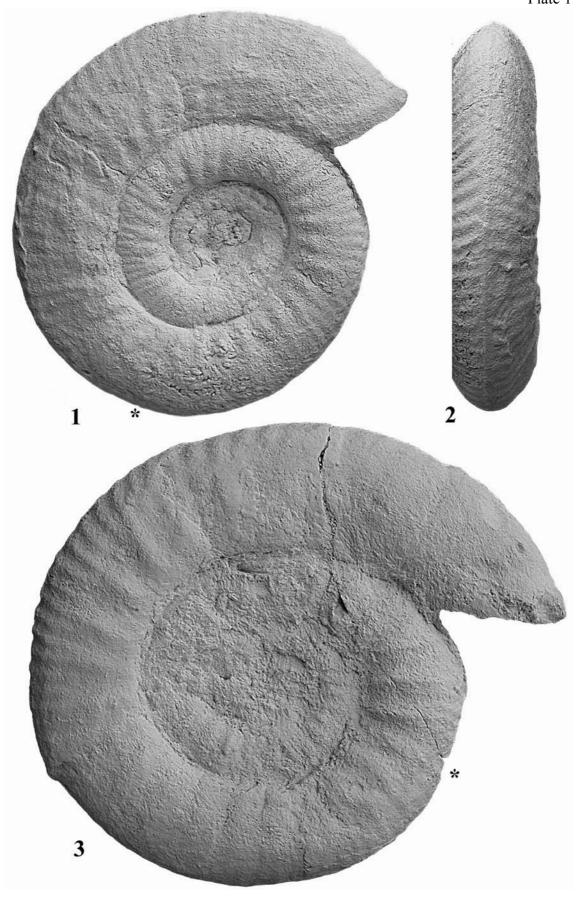


Fig. 1-2: *Cagliceras elaphum* (MERLA), EP95A, Speciosum Zone Fig. 3: *Cagliceras elaphum* (MERLA), EG18A, Opalinum Zone



Fig. 1: Cagliceras elaphum (MERLA), EP84B, Aalensis Zone Fig. 2: Cagliceras crassiventris (MERLA), EB15A, Speciosum Zone

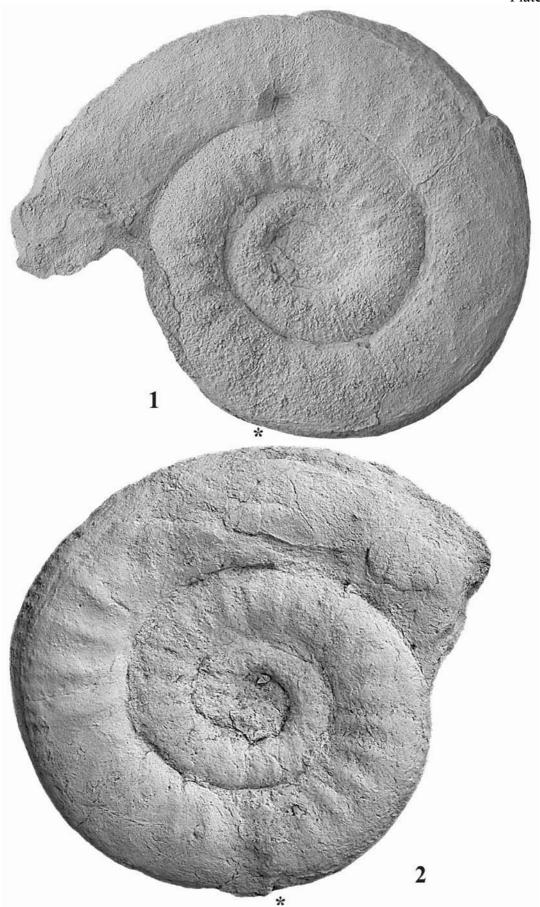


Fig. 1: Cagliceras elaphum (MERLA), EB11, Meneghinii Zone Fig. 2: Cagliceras elaphum (MERLA), EP88, Aalensis Zone

## Plate 4

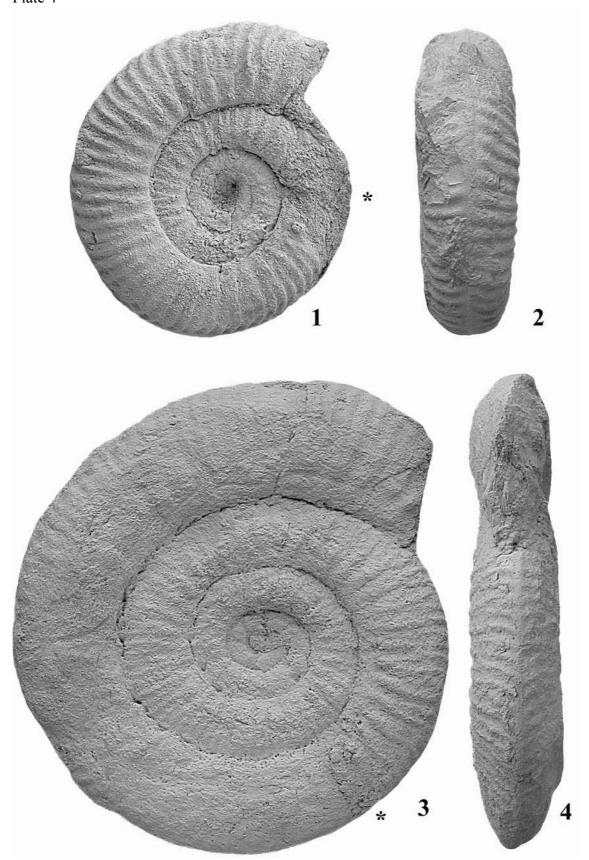


Fig. 1-2: *Cagliceras picenum* (FOSSA-MANCINI), EG54, Speciosum Zone Fig. 3-4: *Cagliceras crassiventris* (MERLA), EP97D, Speciosum Zone

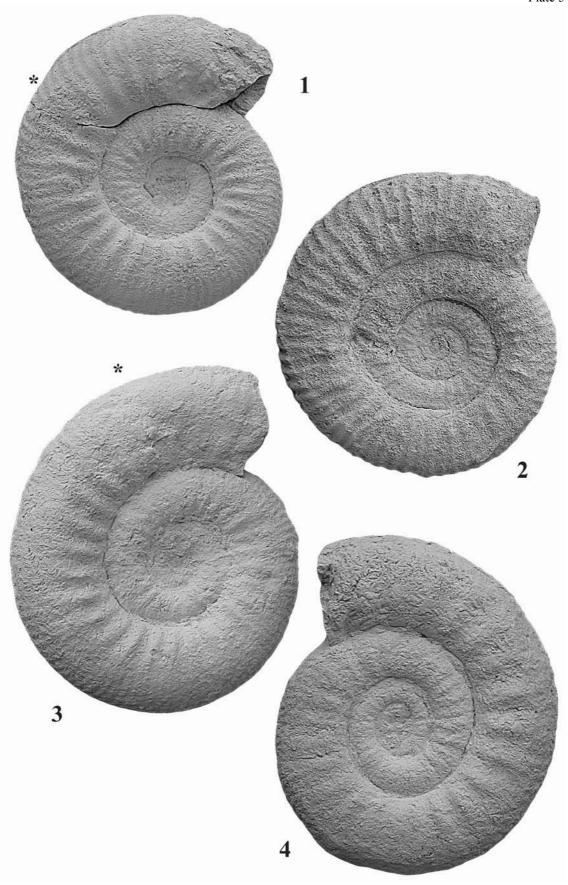
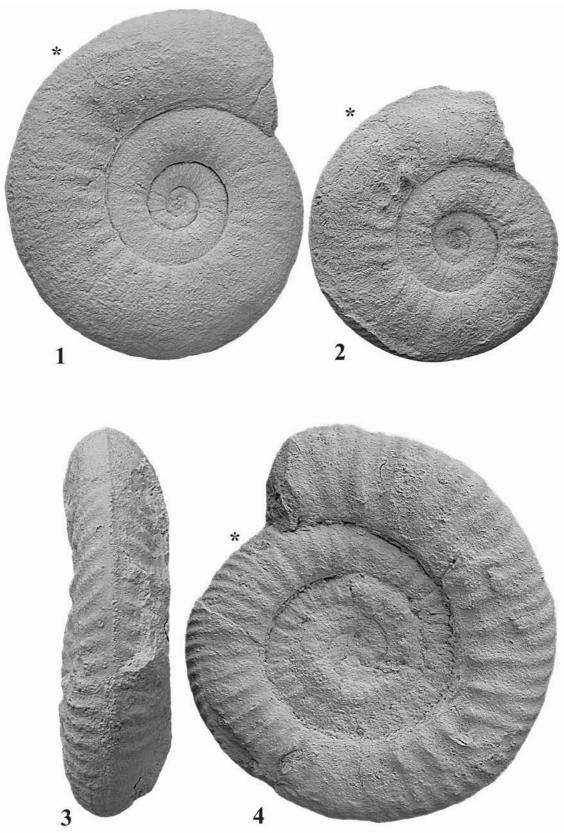


Fig. 1: Cagliceras rotundiformis (MERLA), EG38A, Meneghinii Zone Fig. 2: Cagliceras picenum (FOSSA-MANCINI), EB15B, Speciosum Zone Fig. 3: Cagliceras rotundiformis (MERLA), EG41A, Meneghinii Zone Fig. 4: Cagliceras robustum (MERLA), EP88B, Aalensis Zone

Plate 6



- Fig. 1: Cagliceras costulosum (MERLA), EP84C, Aalensis Zone Fig. 2: Cagliceras costulosum (MERLA), EP84D, Aalensis Zone Fig. 3-4: Cagliceras enigmaticum n. sp., EP97C, Speciosum Zone

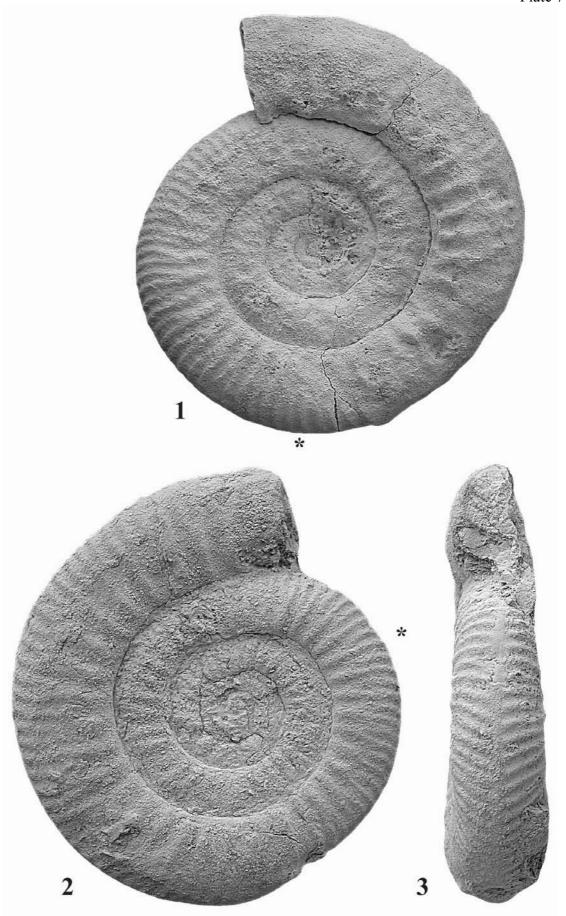


Fig. 1: *Cagliceras enigmaticum* n. sp., EB16, Speciosum Zone Fig. 2-3: *Cagliceras enigmaticum* n. sp., holotype, EP98, Speciosum Zone

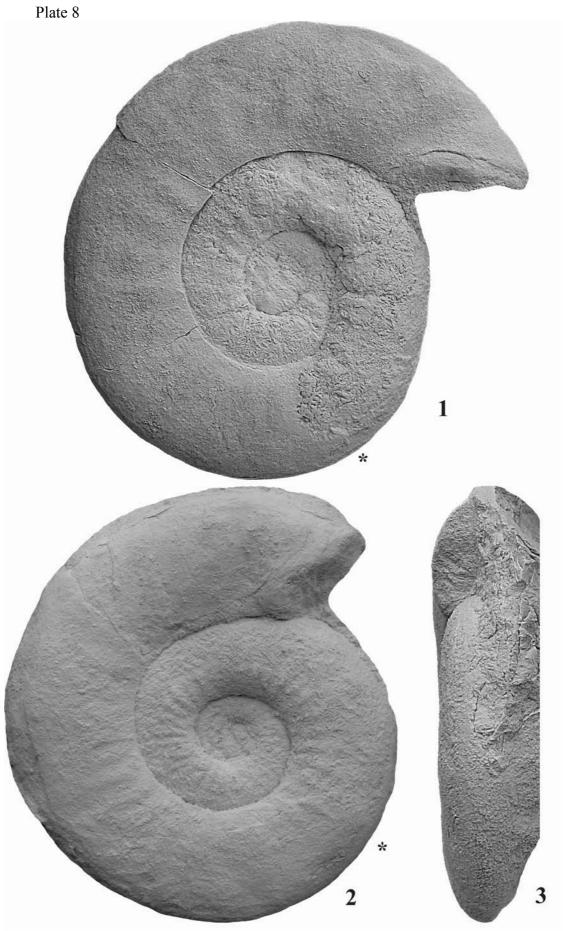


Fig. 1: *Erycites ovatus* GÉCZY, EP78A, Aalensis Zone Fig. 2-3: *Erycites ovatus* GÉCZY, EG7A, Opalinum Zone

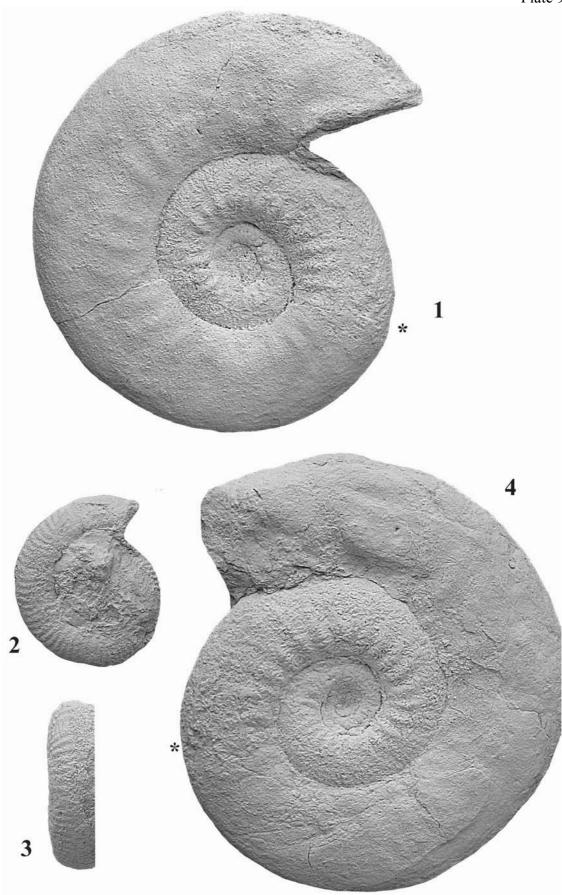


Fig. 1: *Erycites ovatus* GÉCZY, EP79A, Aalensis Zone Fig. 2-3: *Abbasitoides modestus* (VACEK), ETB30B, Murchisonae Zone Fig. 4: *Erycites ovatus* GÉCZY, EG9, Opalinum Zone

Plate 10

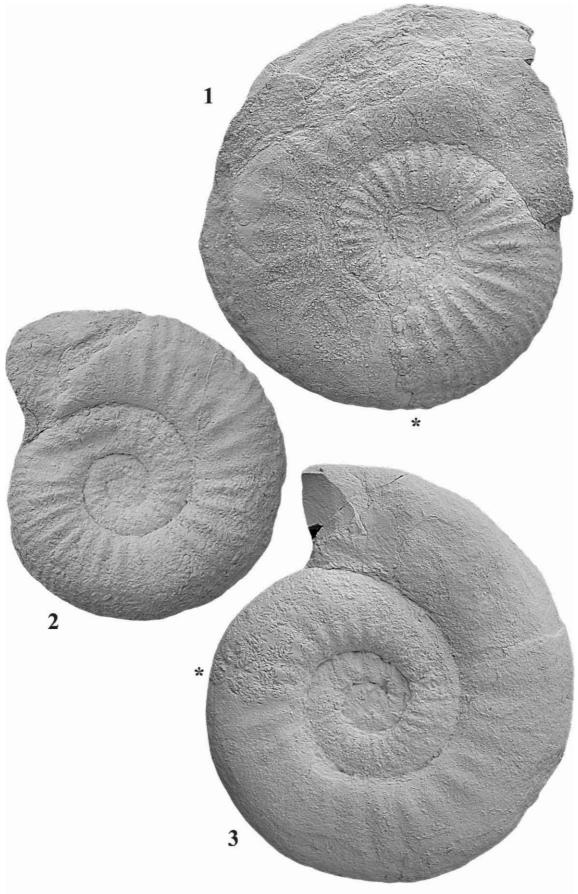


Fig. 1: *Erycites barodiscus* GEMMELLARO, EG19, Opalinum Zone Fig. 2: *Erycites barodiscus* GEMMELLARO, ETA10, Opalinum Zone Fig, 3: *Erycites ovatus* GÉCZY, EP83B, Aalensis Zone

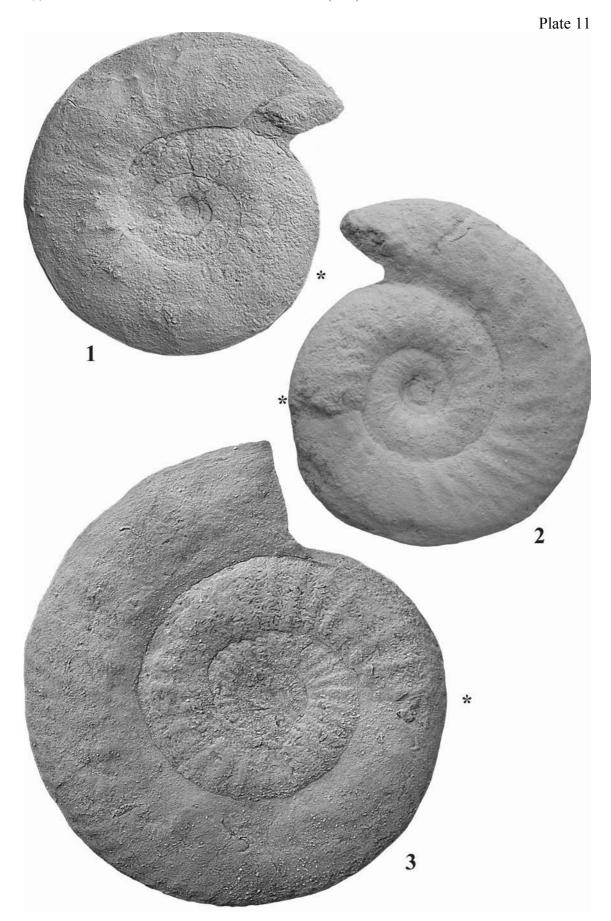


Fig. 1: *Erycites fallifax* ARKELL, EP61, Opalinum Zone Fig. 2: *Erycites fallifax* ARKELL, ETA4, Opalinum Zone Fig. 3: *Erycites barodiscus* Gemmellaro, EP69A, Opalinum Zone

Plate 12

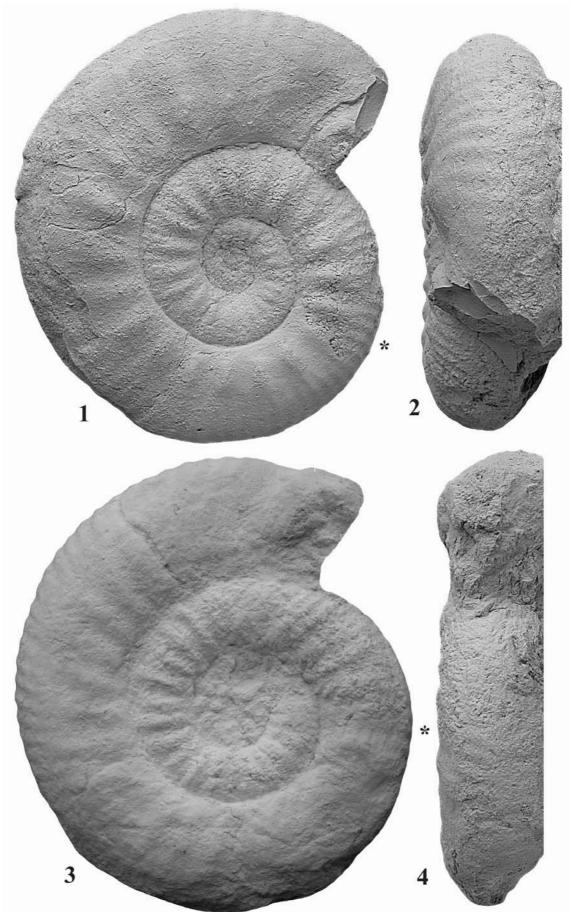
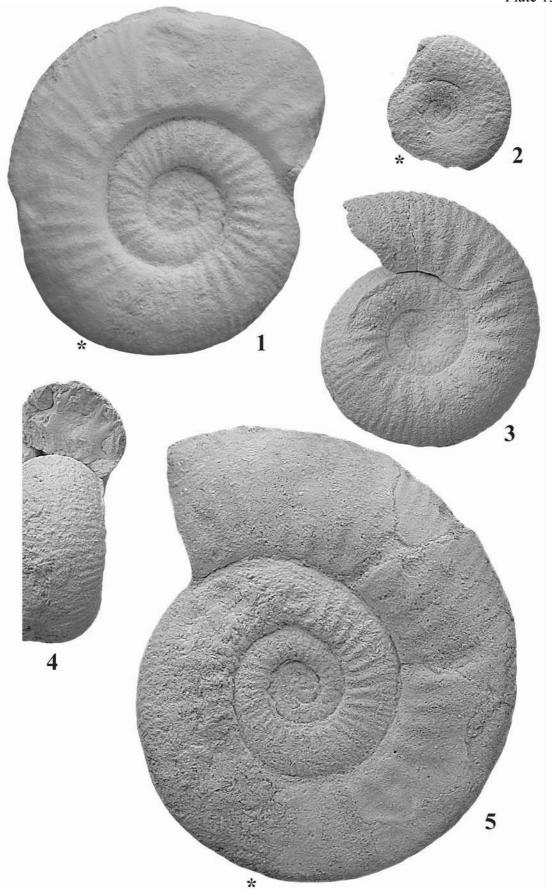


Fig. 1-2: *Erycites gerecsensis* n. sp., holotype, EG31A, Aalensis Zone Fig. 2-3: *Erycites subquadratus* GÉCZY, ETA11B, Opalinum Zone



- Fig. 1: Erycites intermedius Hantken in Prinz, ETB30B, Murchisonae Zone Fig. 2: Abbasitoides modestus (Vacek), ETA7, Opalinum Zone Fig. 3-4: Erycites sp. aff. reussi (Hauer), EG6, Murchisonae Zone Fig. 5: Erycites intermedius Hantken in Prinz, ETB32, Murchisonae Zone