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Taxonomy, dimorphism and phylogenetic significance of the Bajocian (Middle Jurassic) ammonite *Labyrinthoceras*

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RIASSUNTO

Labyrinthoceras, *Spheroceratide bajociano conosciuto in modo incompleto rappresenta un gruppo di ammoniti di notevole interesse avente: distribuzione stratificata ristretta alla zona a Otoites sauzei; distribuzione geografica estesa all'Europa ma con una rappresentante in Alaska; dimorfismo caratteristico; posizione filogenetica vicina all'origine della famiglia Sphaeroceratidae.*

Tutti questi aspetti sono discussi sulla base di un ricco materiale raccolto in Ungheria e su di una revisione di esemplari conosciuti in letteratura o trovati in vecchie collezioni. Sono trattate in dettaglio la variabilità, le morfologie e le specie appartenenti a questo genere. È istituito il nuovo sottogenere microconco Manselites *e la discendenza della coppia dimorfa* Sphaeroceras / Chondroceras *è spiegata per pedomorfosi o neotenia.*

Titolo sintetico: Labyrinthoceras

ABSTRACT

Labyrinthoceras, *this incompletely known Bajocian Sphaeroceratid is a remarkable group of ammonites, having stratigraphic range restricted to the Otoites sauzei Zone, geographic distribution extendig to Europe but with one representative in Alaska, characteristic dimorphism, and phylogenetic status close to the origin of Sphaeroceratidae. All these aspects are discussed on the basis of a rich material from Hungary and a review on specimens published in the literature or found in old collections. Variability, sphere of morphology and species of the genus are treated in detail. A new microconch subgenus,* Manselites *is designated, and the descend of* Sphaeroceras/Chondroceras *dimorphic pair is explained by paedomorphosis or neoteny.*

KEY WORDS

Ammonitina, Sphaeroceratidae, Otoitidae, Jurassic, Bajocian, Palaeontology, Biostratigraphy, Evolution, New taxon, Hungary.

INTRODUCTION

Although the Bajocian Sphaeroceratid genus *Labyrinthoceras* was designated neraly 70 years ago, knowledge on its species remained incomplete until recently. Only the studies on Bajocian ammonites of the last 10-15 years called the attention to the significance of this genus.

Labyrinthoceras, this beautiful sphaerocone is remarkable from several aspects. It is an excellent stratigraphic guide-form, it is intermediate in phylogenetic position between the Otoitidae and the true Sphaeroceratidae, it spectacularly represents a type of dimorphism, and it shows an example for ammonite homoeomorphy. It foreshadows in gross morphology the Bathonian-Callovian *"bullati"*, the specialized group of *Bullatimorphites, Rugiferites* and *Kheraiceras.* This similarity was first recognized by Buckman (1882, p. 142), when he thought that the forms what became later *Labyrinthoceras* are continued into the Bathonian with *"Sphaeroceras" bullatum.* Westermann (1956, p. 27) made clear that this similarity is a case of homoeomorphy, and this recognition gained special emphasis by the revised arrangemets of Tulitidae (i.e. the group of Bathonian-Callovian sphaerocones) into superfamily Perisphinctaceae (see Donovan *et al.* 1981).

Recently published data and new material collected in Hungary enabled to make a comprehensive overview on the genus and its species. This paper is aimed to discuss general features, morphological variability, spatial and temporal distribution, dimorphism and phylogenetic position. Some allusions are made on new taxa, but formal descriptions will be presented elsewhere.

GENERAL ACCOUNTS

Labyrinthoceras, as independent genus was introduced by S. Buckman in 1919 to separate previously distinguished forms from the widely used genus *Sphaeroceras.* The newly designated name referred to comparatively big, thick-whorled, densely-ribbed forms with excentrically coiled body chamber, strongly contracted aperture and extremely intricate sutures. However, Buckman was only at the end of a line, because the independence of these forms was implicitly recognized even in 1867 by Waagen, who designated the first species of this group, giving a new name - *Ammonites meniscus* for an ammonite figured by d'Orbigny in 1845.

Sandoval (1983, p. 204) pointed out that *Labyrinthoceras perexpansum,* Buckman's "genotype" is a synonym of *L. meniscum* (Waagen), and this opinion could be now evidenced by statistical studies. Accordingly, the type of the genus is *Amm. meniscus* Waagen, 1867, with the type specimen *Amm. gervillii* (d'Orbigny non Sowerby, 1842-49, pl. 140, figs. 1-2; refigured here in Fig. 1). Unfortunately the original of d'Orbigny's figure seems to be lost. M. H. Gauthier of the Muséum National d'Histoire Naturelle of Paris informed me that the only existing comparable specimen from the material of d'Orbigny is in the Tesson Collection kept in the British Museum (Natural History). This specimen (No. 37268) was mentioned by Parsons (1974, p. 159) as *L. meniscum,* however my examinations revealed that it belongs into an other species, *L. intricatum* Buckman. The general shape shown in the figures, and the features and dimensions mentioned in d'Orbigny's descritpion do not fit this specimen. Thus a search for other specimens in the d'Orbigny collection, or a designation of a neotype from topotypes is necessary. Nevertheless, despite these difficul-

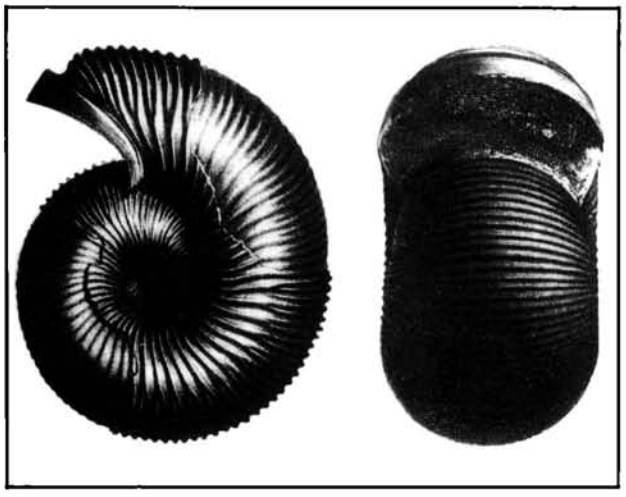

Fig. 1. *Ammonites meniscus* Waagen, the original figures of d'Orbigny (1842-49, pl. 140, figs. 1-2) (0.4x).

ties *L. meniscum* is a well-established species, especially with *L. perexpansum* (Buckman) at hand.

The long hiatus in information about the genus can be probably due to the fact that at first glance these ammonites, especially without body chamber, are very similar to *Emileia*. This Otoitid genus also has dense ribbing, complicated suture-line and excentrically coiled adult whorls. In stratigraphic distribution *Emileia* endures also to the Otoites sauzei Zone, i.e. to the temporal range of *Labyrinthoceras*. However, significant differences do exist in sculpture: *Emileia* has tuberculate or nodate strong primary ribs and its costation fades out on the body chamber, while the ribbing of *Labyrinthoceras* never shows tubercules or nodes, and the ribs endure throughout the body chamber. On the other hand, *Labyrinthoceras* nuclei or incomplete microconchs are difficult to distinguish from small-sized Sphaeroceratids, *e.g. Chondroceras* and *Sphaeroceras*. So the practice in much faunal evaluations to regard small specimens or inner whorls as forms determinable only on generic level probably left many *Labyrinthoceras* unrecognized. At the same time, careful search in formerly collected or described materials may reveal several latent specimens of this genus.

THE SPECIES OF LABYRINTHOCERAS

As it was mentioned above, the first figured specimen of the genus is that on pl. 140, figs. 1-2 in d'Orbigny (1842-49). He interpreted this ammonite as a big *Amm. gervillii* Sowerby, i.e. what is now regarded as *Chondroceras*. Waagen (1867 p. 602), when he established *Ammonites meniscus* n.sp. to this figure, indicated the bigger size, the gradual excentrumbilication and the bifurcating ribs as characteristic and distinguishing features.

The next named species was *Sphaeroceras perexpansum*, which was introduced by S. Buckman (1882, p. 142, pl. 2. figs. 4a-b), with an incomplete phragmocone as holotype. This specimen was refigured later by Buckman in the Type Ammonites (1919 in 1909-30, pls. 134A-B) as the "genotype" of his newly erected genus *Labyrinthoceras*. In the same work he figured subsequently (1921, pls. 134C-D) a beautiful, nearly complete specimen showing the entire body chamber.

Also in 1919, Buckman separated another species from his 1882 "*Sphaeroceras*" *perexpansum* series: a small inner whorl named as *L. intricatum* (pl. 135). A better specimen, an entire form with aperture was obtained later what he figured in 1927 (pl. 135A).

Buckman's Type Ammonites contains further ammonites which he ranged into this genus. In 1921 (pl. 214) he designated *L. extensum*, a small species with fine, tuberculate ribs and ceasing of septation at ca. 30 mm diameter. In 1922 he introduced two additional species: *L. gibberulum* (pl. 278) and *L. amphilaphes* (pl. 279). Both are inner whorls from Dundry, showing fine costation and the former, tiny tubercules.

For several decades no particular work has been made on the genus. In 1964 Westermann (p. 54) revised briefly the group what he regarded as "*Labyrinthoceras - Frogdenites* Dimorphengruppe". He suggested that Buckman's *L. perexpansum, intricatum, amphilaphes* and *gibberulum* are probably synonyms of *L. meniscum* (Waagen), and that *L. extensum* is possibly a *Frogdenites*. Most of these suggestions were later confirmed by Parsons (1974, 1977, 1979) who pointed out that the tuberculate *L. extensum* and *L. gibberulum* are true *Frogdenites* from the topmost Laeviuscula Zone: from the horizon where this small, tuberculate early Sphaeroceratid occurs.

In 1980, after 60 years of the last figure of *Labyrinthoceras*, the first recent photograph of a congeneric from was published. This record (Mariotti *et al.* 1980, pl. 4, fig. 5) refers to a form (*L. perexpansum*) from the Apennines, Italy.

The recent monographs on Spanish material (Sandoval 1983; Fernandez López 1986) gave detailed information on the genus and on the interpretation of its species. It seems to be established that *Labyrinthoceras* has only two generally mentioned European macroconch species, with a dozen figured specimens. However, morphologic variability was not fully analysed, and only some short comments were made on geographic distribution and stratigraphic range.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The first specimens ranged into the genus came from the condensed Lower Bajocian of Normandy and Southern England. Difficult is to decide on which horizon yielded the specimen of d'Orbigny, but most probably it came from the Couche verte (Sauzei Zone). This is the horizon of the specimen in the Tesson Collection, and new collections (see Rioult 1980, p. 79) indicated the occurrence also from this level. Hewever, Waagen (1867, p. 603) mentioned that he collected *L. meniscum* from the topmost beds of the Malière, just below the Couche verte, also of Sauzei Zone age (Parsons 1974).

The English specimens came from Inferior Oolite localities, and the revision of Buckman's sites (Parsons 1974, 1979) cleared that all previous and recent finds are of Sauzei Zone age. Records of the genus from Europe (Ruget-Perrot 1961, p. 55; Pavia 1983, p. 32; Clari & Pavia 1980, p. 87; etc.) indicated similar stratigraphic range. Recent evaluation of the Sauzei Zone faunas (Galácz 1987) established, and newest work on Portugese sections (Fernandez López *et al.* 1987) supported that *Labyrinthoceras* appears at the base and disappears at the top of this zone, and in this way it is a very useful

ammonite to identify the Sauzei Zone.

Outside Europe there is only a single known occurrence of *Labyrinthoceras*, in North America, from where Imlay (1964, p. B41, pls. 9-10) reported firstly on the genus. His new species *L. glabrum*, especially the inner whorls, are very similar to the European forms, the difference is that the Alaskan species has slender whorls and less complicated suture-line. The horizon of *L. glabrum* corresponds to the Sauzei Zone. Sandoval (1983, p. 207) suggested that "*Otoites? filicostatus* n. sp." (Imlay 1964, p. B30, pl. 14, figs. 9-11) may be the microconch of *L. glabrum*. These tiny lappeted forms came from an other locality of the Cook Inlet region, from rocks ranged also into the Sauzei Zone.

The two European species of *Labyrinthoceras* have different stratigraphic ranges. *L. intricatum* is restricted to the lower part of the Sauzei Zone (Kumaterus Subzone, Galácz 1987), *L. meniscum* ranges through the whole zone.

STUDIES ON HUNGARIAN MATERIAL

The Bajocian sections studied recently in the Transdanubian Central Range (W Hungary) yielded an exceptionally rich *Labyrinthoceras* material. Two Bakony Mts. localities (Lókút Hill and Gombáspuszta) gave specimens of very good preservation, and additional examples were studied also from the Gerecse Mts. (near Budapest). From the localities the material totalled in nearly 100 specimens, and these gave a good basis for detailed studies on variability.

Most of the specimens are macroconchs. Variability is remarkable, but the two species: *L. meniscum* and *L. intricatum* are clearly distinct in size and whorl-width (Fig. 2). *L. meniscum* is a bigger form with 90 to 140 mm maximal diameter, while *L. intricatum* has smaller adult diameter. The two forms are distinguished from very early growth stage: there is a difference in whorl-thickness from ca. 40 mm, where *L. mensicum* is extremely depressed and wide, showing 100% whorl-breadth in proportion of the diameter. This difference prevails throughout the shell. The umbilicus of *L. intricatum* is wider on the last whorl and its body chamber (ca. 1 whorl) is contracting rapidly. The body chamber contraction of *L. meniscum* is rather gradual, following the same excentrumbilication that begins on the phragmocone.

The measurements on museum specimens and published forms (Fig. 3) gave the same results. Most signifi-

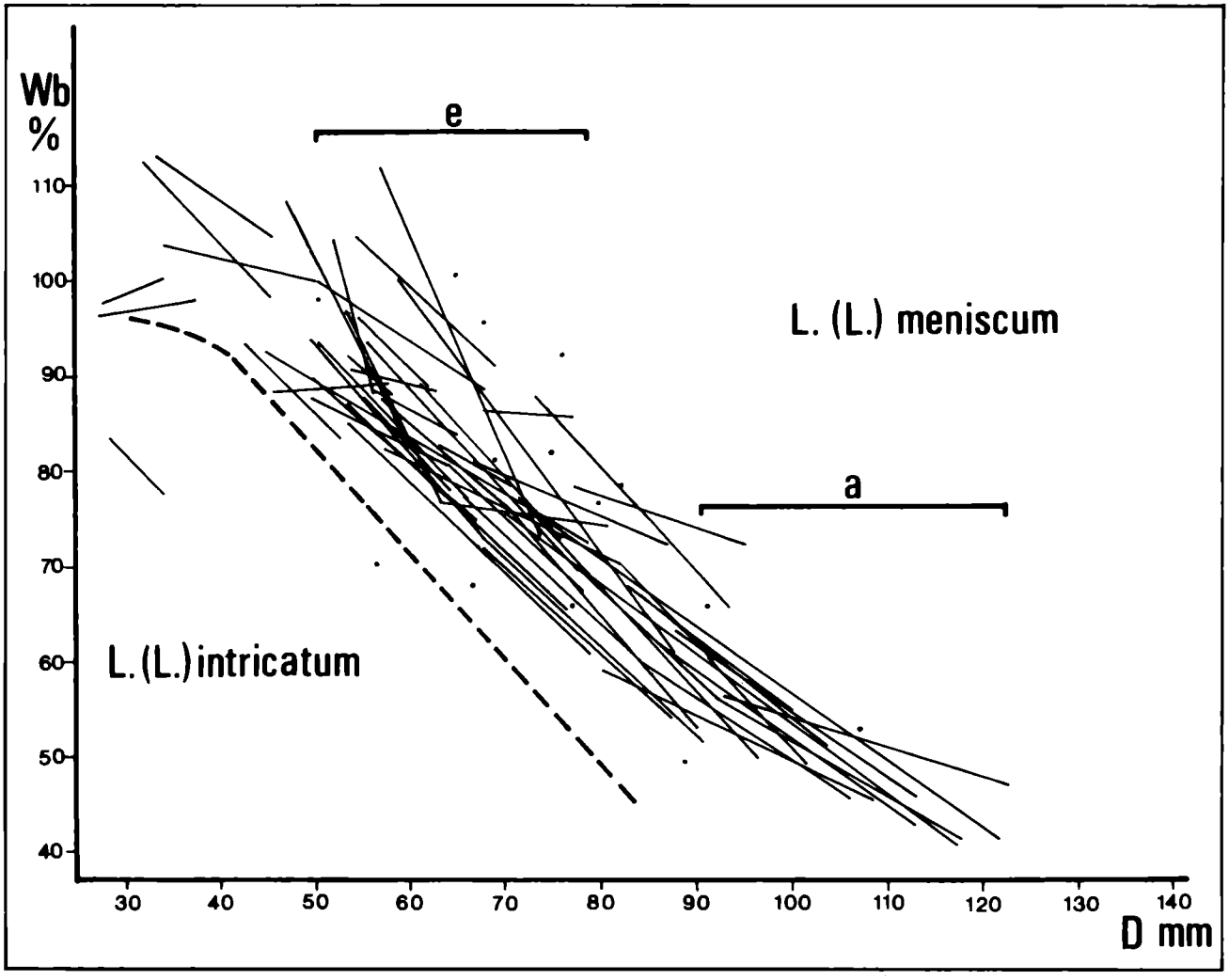

Fig. 2. Diagram of whorl-breadth (Wb) plotted against diameter (D) for *Labyrinthoceras* specimens from localities in the Transdanubian Central Range (Hungary). e = end of phragmocone; a = aperture.

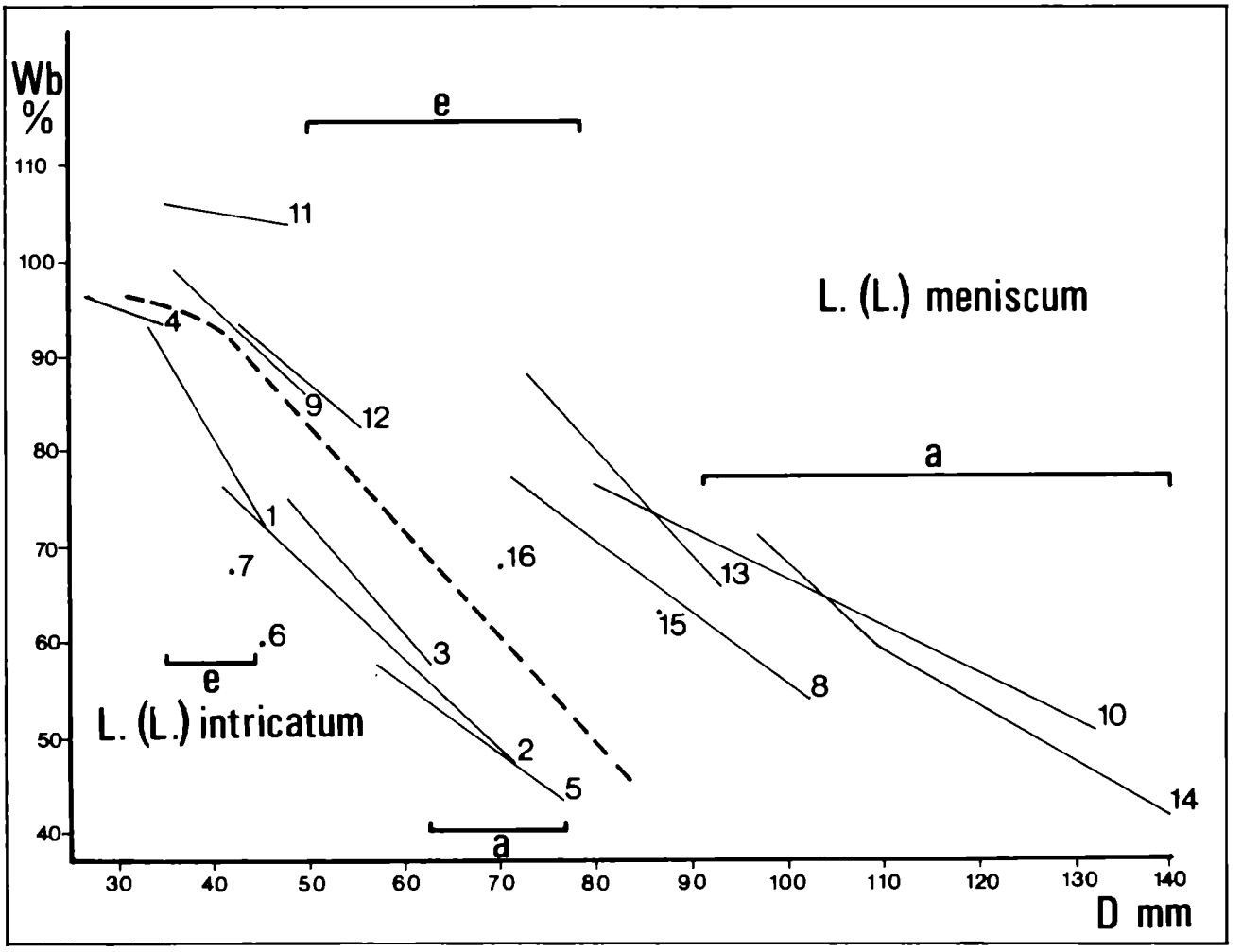

Fig. 3. Diagram of whorl-breadth (Wb) plotted against diameter (D) for *Labyrinthoceras* specimens figured in the literature or found in museum collections. e = end of phragmocone; a = aperture. 1: *L. intricatum*, holotype (Buckman 1919, pl. 135); 2: *L. intricatum* paratype (Buckman 1927, pl. 135A); 3: *L. intricatum* from St. Vigor (Tesson Coll., British Museum (NH), 37268); 4: *L. intricatum* from Sherborne, (Geological Survey Museum, London, 3536); 5: *L. intricatum* (Sandoval 1983, pl. 5, fig. 3); 6: *L. intricatum* (Fernandez López 1986, pl. 40, fig. 1); 7: *L. intricatum* (Fernandez López 1986, p. 370); 8: *L. meniscum*, holotype (d'Orbigny 1842-49, pl. 140, figs. 1-2); 9: *L. perexpansum*, holotype (Buckman 1919, pl. 134); 10: *L. perexpansum*, paratype (Buckman 1921, pls. 134C-D); 11: *L. amphilaphes*, holotype (Buckman 1922, pl. 279); 12: *L. meniscum* from Sherborne (Sedgwick Museum, J20155); 13: *L. meniscum* from Sherborne (Sedgwick Museum, J24530); 14: *L. meniscum* (Sandoval 1983, p. 203); 15: *L. meniscum* (Sandoval 1983, p. 203); 16: *L. meniscum* (Sandoval 1983, pl. 4, fig. 4).

cant that there is no overlap in the adult sizes: *L. intricatum* is consequently smaller than *L. meniscum*.

The sculpture is similar in both species of *Labyrinthoceras*: fine, dense, prorsiradiate, non-tuberculate ribs with no sign of fading on the body chamber. *L. meniscum* has generally 50 to 70 inner ribs on the middle and outer whorls, depending on individual size. Most inner ribs split into two secondaries high on the flanks. There is no significant difference in the strength of inner and outer ribs. *L. intricatum* has fewer ribs, mainly because of smaller size. The ribbing of this species is slightly sinuous, because the prorsiradiate inner ribs give rise to secondaries tending to be radial ventrally.

Morphological studies on associated microconchs resulted in distinguishing two forms (see below), also on the basis of average size, style of coiling and shape of whorl-section.

A significant result of the studies is the morphological stability of these froms. Attempted grouping of measured characters or sculptural elements by stratigraphic levels or localities did not reveal any traceable trend to suggest microevolutionary changes. This recognized stability is demonstrated by the overlap of morphologic data obtained from Hungarian material and from the randomly given specimens of different occurrences and horizons from the European Sauzei Zone.

DIMORPHISM OF LABYRINTHOCERAS

The first to suggest dimorphism for *Labyrinthoceras* was Westermann (1964), who proposed *Frogdenites* Buckman as corresponding micrconch. This was dismissed later by Parsons (1977) on stratigraphic grounds. A suggestion made on the basis of morphologic similarities (Galácz 1980, p. 77) indicated *Amm. manselii* J. Buckman as possible microconch.

Though slowly, information on dimorphism has accumulated in the literature, especially in the last years. Parsons (1979, p. 138) mentioned "*Labyrinthoceras* aff. *meniscum* (Waagen), microconch" from the Brown Iron-

shot of Dundry. The ammonite described by Sandoval (1983, p. 206, pl. 3, fig. 4), as belonging to an unnamed microconchiate subgenus of *Labyrinthoceras* seems to be rather a microconch *Kumatostephanus*. Fernandez López (1986, p. 369) agreed on to regard *Amm. manselii* as a microconch *Labyrinthoceras*, and he figured a fragmentary specimen of this species (pl. 40, figs. 4a-b). On the other hand, the "*Labyrinthoceras*" sp. nov. 1 of Fernandez López (pl. 40, fig. 2) is an other microconch of problematic affinity.

In the Hungarian material *Labyrinthoceras* occurs together with small, finely-ribbed, non-tuberculate microconchs. This is the group of the rarely represented, but long recognized ammonites of which first specimen had been described by J. Buckman in 1881 as *Ammonites manselii*. Unfortunately, the type specimen seems to be lost (H. Torrens, pers. comm.), but subsequent description given by S. Buckman (1881, p. 598) and the figures (S. Buckman 1882, pl. 2, figs. 3a-b) are sufficient to maintain this species (Fig. 4).

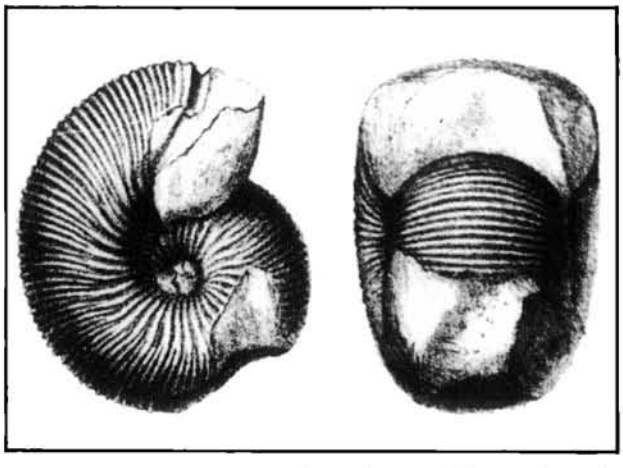

Fig. 4. *Ammonites manselii* J. Buckman, the original figures of S. Buckman (1882, pl. II, figs. 3a-b).

One of the distinctive and rather important features of *Amm. manselii* is the peculiar aperture. All three early descriptions emphasized the presence of a deep preapertural constriction on the wide, ventrally flat mouth-border. There is no mentioning of lappets. The unlappeted but laterally flared, sinuous apertural margin is very similar to those illustrated by Sturani (1971, fig. 42) in microconch *Sphaeroceras*.

Using the informations and figures of *Ammonites manselii*, it is possible to identify true microconchiate *Labyrinthoceras* in museum collections. In the Sedgwick Museum (Cambridge) there are two "*L. intricatum*" specimens (J20154, J24526) from Sherborne, previously labelled as *Sphaeroceras* sp., which are apparently microconch *Labyrinthoceras*. Careful search in the literature may reveal additional, even figured microconchiate specimens. One probable example is the "*Sphaeroceras gervillii*" recorded by Maubeuge (1951, pl. 12, figs. 5a-c) from the Sauzei Zone.

All these considerations point out that, though generally unrecognized, microconch *Labyrinthoceras* do exist as a coherent group, and occur together with traditional macroconchs. The earlier records and the rich material available from Hungary enable to designate a new subgenus of *Labyrinthoceras: Manselites* n. subg., with type species *L. (Manselites) manselii* (J. Buckmann, 1881).

At the moment two independent forms can be distinguished within *Manselites*. The type species *L. (M.) manselii* is more common and occurs usually with *L. (L.) meniscum*. This pairing as corresponding dimorphs seems evidenced by their morphologic similarity: bigger size, slower and more gradual umbilical excentricity. The probable microconch pair of *L. (L.) intricatum* has smaller average size and stratigraphic range being restricted to the lower part of the Sauzei Zone.

Being of special importance, calculations were made on dimorphic size ratios. The measured macroconch *Labyrinthoceras* specimens (see Figs. 2 and 3) have the aperture at 91 to 140 mm (*L. meniscum*) and between 50 and 79 mm (*L. intricatum*). The corresponding microconchs show the respective values as 36 to 45.5 mm (in *M. manselii*) and 35.5 to 45 mm in the pair of *L. (L.) intricatum*. The ratios for the averages give 116/41 = 2.8 and 70/38 = 1.8, respectively. These values are significantly lower than those of *Emileia* - *Otoites* (ca. 6.0 to 10.0) and of *Emileites* - *Trilobiticeras* (ca. 4.0 - 6.5), but quite close to that of *Frogdenites* macro-and microconchs.

PHYLOGENETIC STATE AND SIGNIFICANCE

Labyrinthoceras is long thought as having important phylogenetic position. Arkell (1951-59, p. 78) suggested *Labyrinthoceras* as a possible ancestor of *Sphaeroceras*, and, accordingly, he placed the genus into the Sphaeroceratidae (Arkell *et al.* 1957, p. L292), following a practice initiated by Buckman (1920, p. 22). Nevertheless, *Labyrinthoceras* is very similar to *Emileia*, thus some authors (e.g. Fernandez López 1986, p. 368) classified it as Otoitid. The latest classification (Donovan *et al.* 1981, pp. 146-147) ranged *Labyrinthoceras* into Sphaeroceratidae, emphasising its intermediate characters differentiating from those of Otoitidae.

Labyrinthoceras differs from Otoitidae with its sculpture, however Arkell stated that inner whorls are inseparable from that of *Emileia*. On the other hand he regarded their sutures as different, *Labyrinthoceras* having thick-stemmed second lateral lobe. This feature was his ground to originate *Labyrinthoceras* (and Sphaeroceratids) from *Docidoceras* (Arkell 1951-59, p. 82 and table III on p. 75). Although, phylogenetic value of the broad, blunt second lateral lobe, which guided Arkell to place Tulitids into the Sphaeroceratidae is seriously questioned by the now generally accepted view that Tulitidae are specialized Perisphinctids (see Hahn 1971 and Donovan *et al.* 1981, pp. 151-152).

The problem of systematic position of *Labyrinthoceras* could be easily solved if one regards dimorphic features as decisive. The loss of lateral lappets in adult microconchs distinguishes all Sphatnoceratidae from Otoitids which have typical lateral auricles in early and later microconchs (e.g. *Trilobiticeras* and *Otoites*). The disappearance of lappets probably occurs even in *Frogdenites*, of which first undoubted microconchs were figured recently by Fernandez López (1986, pl. 40, figs. 5-6), as *Frogdenites* n. sp. These small forms are adults at 18 and 22 mm, and though fragmentary, they show no indication of lappet. The only reference to lappeted *Frogdenites* is a drawing of microconch *F. spiniger* by Parsons (1977, in fig. 3).

.However, the type of this species (Buckman 1909-30, pl. 215) is a big, but incomplete specimen, and a comparable form from Hungary (Galácz 1982) had only a flared peristome but apparently no lappet.

Consequently, *Labyrinthoceras* is a Sphaeroceratid by its dimorphism, while some other features (incl. the complex suture-line) are very similar to *Emileia* and corresponding microconchs. The actual connection with Laeviuscula Zone *Emileia* species, the probable ancestors, is uncertain. *Labyrinthoceras*, which appears suddenly at the base of the Otoites sauzei Zone with at least two differentiated species has probably no direct connection with *Frogdenites* - an other descendant of *Emileia* (or *Emileites*) (Fig. 5). At the present, when all Otoitids need a complete, stratigraphically controlled revision, more precise statements on immediate ancestors cannot be made.

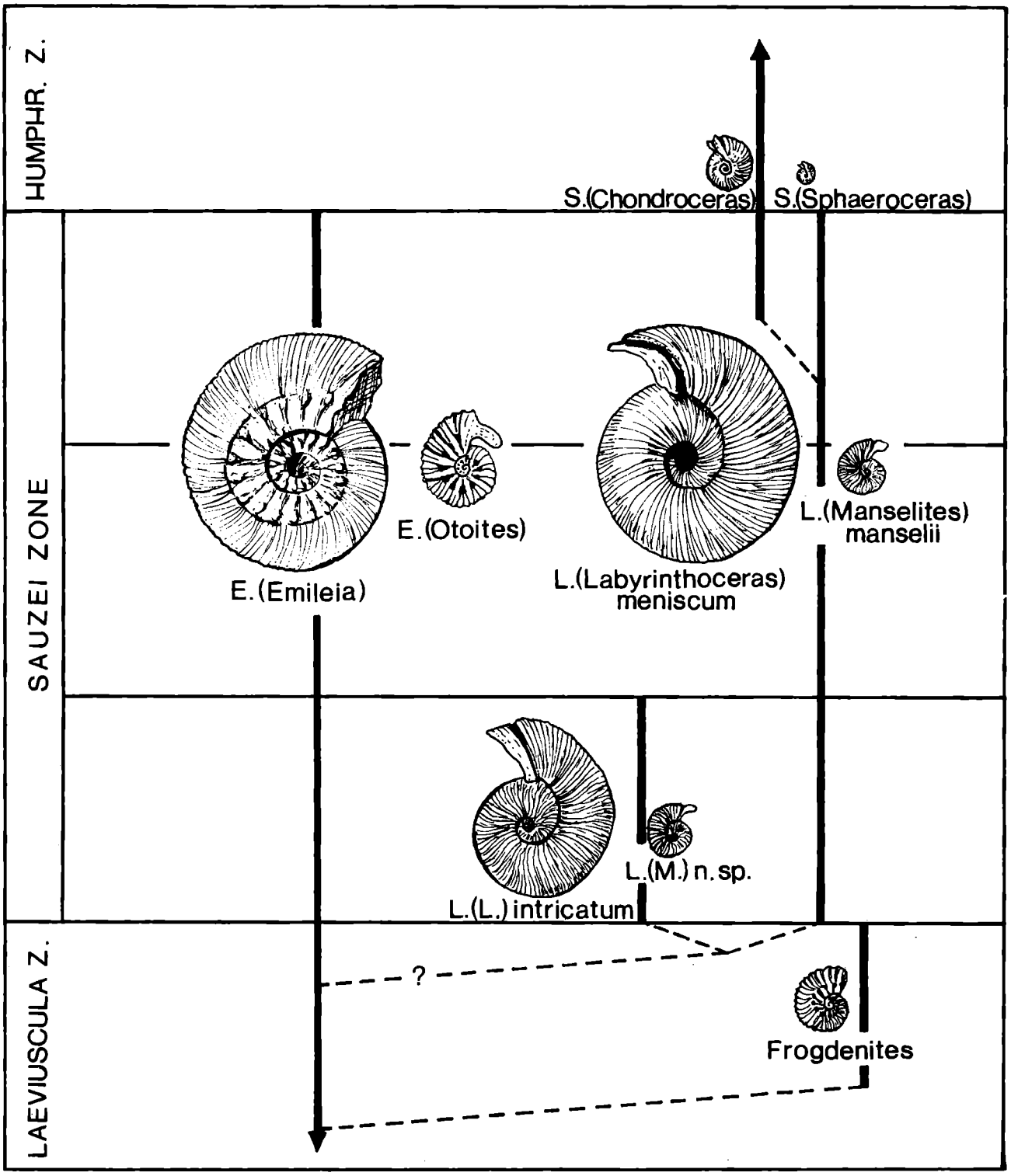

Fig. 5. Some Otoitid (left) and Sphaeroceratid (right) ammonites and their possible relations in and around the Lower Bajocian Otoites sauzei Zone.

As an alternative origination, the Pacific subgenus *Chonromileia* can be indicated. These forms as *Emileia*-related sphaerocones were designated by Westermann and Riccardi (1979, p. 129) in Andean Laeviuscula and Sauzei Zone faunas. The macroconchs are medium-sized, *Emileia*-like forms with excentric body chamber, forwardly-inclined peristome, distant primary ribs and loss of nodes on the last whorl. The microconchs are *Otoites* - like, strongly ribbed and moderately tuberculated, with lappeted aperture. Thus the style of dimorphism is of true Otoitid, very close to *Emileites/Trilobiticeras*. If *Labyrinthoceras* has evolved from *Chonromileia*, a transitional form would have been *L. glabrum* Imlay. Then the genus left the Pacific realm, and might have appeared suddenly in Europe. This would explain the missing apparent transitions in the latter area.

Similarly interesting is the connection between *Labyrinthoceras* and younger Sphaeroceratids. *Sphaeroceras* (and its macroconchiate subgenus *Chondroceras*) is long considered as derivatives of *Labyrinthoceras*; Spath (1936, p. 13) even placed them into the same genus, *Sphaeroceras*. This is an exaggeration of the similarities (see Arkell 1951-59, p. 78), however the close relationship was never denied. One of the few exceptions is the opinion of Sturani (1971, p. 136), who regarded *Chondroceras* and *Sphaeroceras* as direct descendants of *Frogdenites*, by the loss of lateral tubercules. Nevertheless, loss of nodes appear even in *Labyrinthoceras*, and the associated characters, i.e. basically similar suture, apertural features and dimorphic size ratios, make dimorphic *Sphaeroceras* as a tiny edition of *Labyrinthoceras*.

Intermediate forms, again, are unknown. Pavia (1983, p. 156) suggested "*Sphaeroceras*" *dzirulense* Kakhadze (1943, p. 308, pl. 7, figs. 1-5) as a possible transitional form, but the "type series" of Kakhadze shows typical *Sphaeroceras* and *Chondroceras* specimens, of which Sauzei Zone age is rather problematic.

The abrupt appearances of related new forms, where the prevailing morphology is associated with sudden size decrease may suggest paedomorphic evolutionary event. Classic examples of ammonite paedomorphosis have been demonstrated as false by several authors (see in Kennedy 1977), however unfortunate cases do not discredit the model completely. Paedomorphosis and / or neoteny can successfully explain the origin of several cryptogenic forms. So the descend of small, but morphologically comparable *Chondroceras* and *Sphaeroceras* is regarded here as a neotenic development from *Labyrinthoceras* and *Manselites*, which took place in the middle of the Otoites sauzei Zone.

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