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### On the true stratigraphic position of *Macrocephalites macrocephalus* (SCHLOTHEIM, 1813) and the nomenclature of the standard Middle Jurassic "Macrocephalus Zone"

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With 10 plates, 13 textfigures and 1 table

#### Summary

A new section is described in the mainly Lower Callovian "Macrocephalen-Oolith" of the Ipf, near Bopfingen, at the northeastern end of the Swabian Alb. Large collections of ammonites made bed by bed are listed. They include *Macrocephalites macrocephalus* (SCHLOTHEIM, 1813) at its newly discovered type locality. It turns out that this species, index of the standard Macrocephalus Zone and Subzone in its modern restricted sense and characterizing a well-defined *macrocephalus* faunal horizon, does not occur in its nominal Zone but higher: in the overlying Koenigi Zone. The name of the Macrocephalus Zone must therefore be changed.

The history of the Macrocephalus Zone since its introduction by OPPEL in 1857 is reviewed. A substitute name for the Zone is proposed: the Herveyi Zone, index *Macrocephalites herveyi* (J. SOWERBY, 1818). The systematics of some species of the *macrocephalus* horizon important for correlation are discussed. They include species of *Reineckeia*, *Proplanulites*, *Kepplerites*, *Chamoussetia* and *Bullatimorphites*, as well as *M. macrocephalus* itself. Two new names are introduced: *Bullatimorphitinae* subfamilia nova of the Tullitidae BUCKMAN, 1921; and *Reineckeia quenstedti* nomen novum pro *Amm. franconicus* QUENSTEDT, 1886, non SCHLOTHEIM, 1813, whose type locality is also at the Ipf.

#### Zusammenfassung

Vom Ipf bei Bopfingen, nordöstliche Schwäbische Alb, wird ein neues Profil aus dem Macrocephalen-Oolith, überwiegend Unter-Callovium, beschrieben. Umfangreiche horizontierte Aufsammlungen von Ammoniten werden aufgeführt. Sie enthalten *Macrocephalites macrocephalus* (SCHLOTHEIM, 1813) von seiner kürzlich entdeckten Typuslokalität. Daraus folgt nun, daß diese Art, Indexart der im modernen Sinne enggefaßten Standard-Zone und -Subzone des *M. macrocephalus*, einen gut definierten *macrocephalus*-Faunenhorizont belegt. Dabei zeigt sich allerdings, daß *M. macrocephalus* nicht in seiner Nominat-Zone vorkommt, sondern höher, in der darüberfolgenden Koenigi-Zone. Deshalb muß der Name der Macrocephalus-Zone geändert werden.

Die Geschichte der *Macrocephalus*-Zone seit ihrer Einführung durch OPPEL (1857) wird dargelegt. Ein Ersatzname für diese Zone wird vorgeschlagen: *Herveyi*-Zone, Indexart *Macrocephalites herveyi* (J. SOWERBY, 1818). Die Systematik einiger Ammoniten aus dem *macrocephalus*-Horizont, die für die Korrelation besonders wichtig sind, wird diskutiert. Es sind dies besonders Arten der Gattungen *Reineckeia*, *Proplanulites*, *Kepplerites*, *Chamousetia* und *Bullatimorphites* sowie natürlich *M. macrocephalus* selbst. Zwei neue Namen werden eingeführt: *Bullatimorphitinae* subfamilia nova der *Tulitidae* BUCKMAN (1921) und *Reineckeia quenstedti* nomen novum pro *R. franconica* (QUENSTEDT, 1886 non SCHLOTHEIM, 1813), deren Typuslokalität ebenfalls der Ipf ist.

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### 1. Introduction

The name *Ammonites macrocephalus* SCHLOTHEIM, 1813, is one of the most venerable. Ammonites ascribed to this species were familiar to every collector in Bavaria and Württemberg from the earliest days of palaeontology, even though there were no usable figures before those published by ZIETEN (1830). The importance of these ammonites was acknowledged by v. BUCH (1829) in the first attempt to classify all the forms then known into higher categories of naturally related groups, or families. The "Macrocephali" were one of the nine families he recognized, increased a year later to fourteen (v. BUCH 1832). The taxonomic anomaly in which the numerous species of the single genus *Ammonites* were distributed over so many families was resolved in the case of the "Macrocephali" by ZITTEL (1884), who founded the genus *Macrocephalites* much as we use it today. Finally, the "Macrocephali" were formally ratified as a family *Macrocephalitidae*, based on a valid type genus according to the

Rules of Nomenclature, by SALFELD (1921). SCHLOTHEIM's species is therefore central to an important area of ammonite taxonomy.

The value of the "Macrocephali" as guide-fossils ("Leitmuscheln" of v. BUCH, 1839), characteristic of a sharply defined horizon near the top of the Brown Jura, was pointed out by QUENSTEDT (1843: 359). He refers explicitly to the "Macrocephalus-schicht", only a few feet thick, recognizable everywhere from the Rhine to the Nördlinger Ries, and hence of great stratigraphical value. It was the first of many similar formational names subsequently introduced in various parts of Germany and elsewhere, such as "Macrocephalen-Bank", "Macrocephalen-Oolith" etc. (see e. g. WESTERMANN, 1967). Lastly, SCHLOTHEIM's species found a place as index-fossil in the first attempts at a general chronostratigraphic classification of the Jurassic rocks of Europa by D'ORBIGNY (1850: 600 et seq.) and OPPEL (1856–58). Adopting the "étages" of D'ORBIGNY as major divisions of the "Juraformation" (the Jurassic System of today), OPPEL subdivided the "Kellowaygruppe" ("l'étage Callovien" of D'ORBIGNY) further into three zones (p. 506): "Zone des *Amm. macrocephalus*" (lowest); "Zone des *Amm. anceps*"; and "Zone des *Amm. athleta*" (highest). These three zones correspond quite closely to our Lower, Middle and Upper Callovian Substages of today. Each of these was in turn subdivided further, but there remained both a restricted *Macrocephalus* Zone and a *Macrocephalus* Subzone in the standard chronostratigraphical zonal scale currently in use for the Northwest-European Province, which in the Callovian includes all of extra-alpine Germany and Switzerland. SCHLOTHEIM's species is therefore also of great importance in stratigraphy, both as guide-fossil and as zonal index.

Since OPPEL's time there has been great progress, and it seems that we may now be in sight of the limits to what is achievable. The history of *Amm. macrocephalus* both in systematics and its use in stratigraphy is complicated. It illustrates almost all the principles of zoological classification, zoological nomenclature, biostratigraphy and chronostratigraphy. It provides therefore classic examples of the importance of these principles and the need for their proper understanding.

Palaeontologically, to be able to claim that our knowledge of an ammonite species such as *Macrocephalites macrocephalus* is complete, it has to-day to fulfil four requirements.

Firstly, it has to have a typological definition, i. e. a type specimen. Choice of this, if not clear from the original definition, is regulated by the International Code of Zoological Nomenclature (1985).

Secondly, we have to have an assemblage of topotypes – specimens from precisely the same faunal horizon and locality as the type – to map out the morphological and ontogenetic variability of the fossil species, including its possible dimorphism. We then assume that such an assemblage approximates to what had been an isochronous, instantaneous biospecies. This delimits what is sometimes called the horizontal extent of the species.

Thirdly, we have to have a stratigraphical succession of such assemblages to see how the species changed with time. This establishes the vertical extent or range, and hence temporal duration, of the chronospecies.

Fourthly, we need to know the geographical extent of the species in at least its type horizon, to be able to identify possible endemisms in faunal provinces, and hence geographical subspecies, races or local populations. This requirement is always by far the most difficult to meet because of the incompleteness of the geolo-

gical record. It is however important only in detailed studies of evolutionary systematics, and need not concern us further here.

Stratigraphically, we are interested in refining the time-resolution of the geological record through the biostratigraphy of the guide-fossils, here the ammonites, whose correlations over useful distances transcend local variations of lithology and palaeoecology. There are two tasks. The first is to characterize as many distinguishable faunal horizons as possible, no matter how local (QUENSTEDT 1843). The second is to arrange these in stratigraphical order and to construct from them a standard chronostratigraphical scale of Stages, Zones and Subzones that may be used as a standard of reference in dating rocks regionally and internationally (OPPEL 1856–58). For a recent review of principles and methods see CALLOMON 1985a. Such a scale is refined by successive subdivision. To give an idea of the progress achieved since OPPEL's time, the number of Zones, the finest subdivisions he used, in his great tables of 1858 (§ 119–20, nos. 63, 64) was 33. Today the standard zonations of the region he considered divide the Jurassic into about 76 Zones and 155 Subzones. The number of distinguishable faunal ammonite horizons recognizable more locally is over 500. This gives us time-resolutions of the order of 100 000 years.

To define fully a standard chronostratigraphic unit requires three separate steps.

The first is the identification of the characteristic assemblages of guide-fossils and their horizons (“... jeglicher Horizont, der an einem Orte durch eine Anzahl für ihn constanter Species markirt wird, auch in der entferntesten Gegend... wieder zu finden sei. Diese Aufgabe ist zwar eine schwierige [sic]...“ – OPPEL 1856: 3).

The second step is the typological definition of the unit in terms of its boundaries by means of markers in selected type sections, the boundary stratotypes. In a stan-

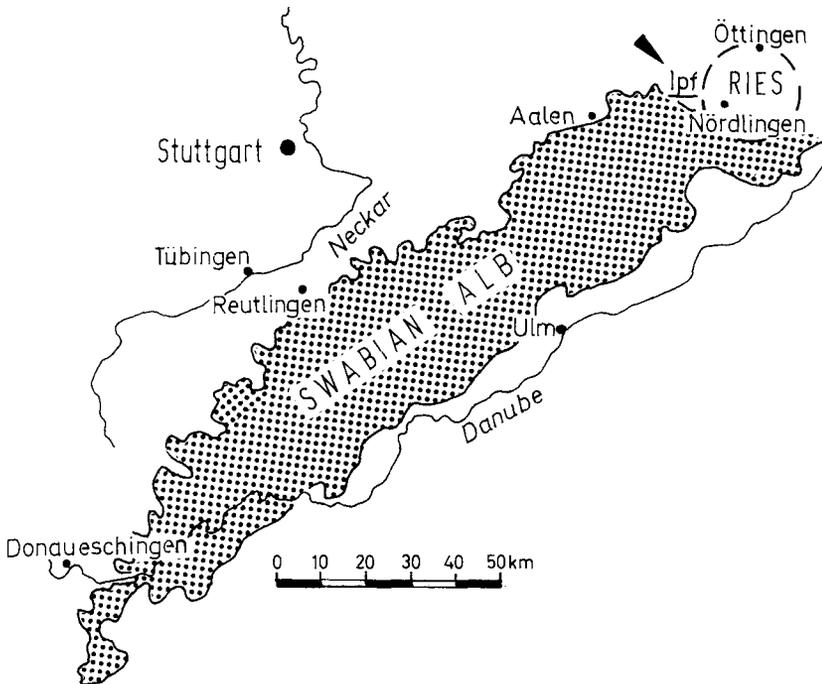


Fig. 1. Map of the Swabian Alb (shaded), SW-Germany, with the Ipf near Bopfingen.

dard scale, units are defined by their bases. Their tops are automatically defined by the bases of the next higher units in the scale.

The third step in defining a standard Zone is the selection of one of the guide-fossils as name-giving index species. The index may but need not be particularly characteristic of the Zone. Neither need its range coincide with that of its nominal Zone, nor need it even be restricted to it. Its only function is to name the stratigraphical unit (cf. OPPEL 1858: 813). But it should at least occur in its Zone: hence, to be certain, its type should have come from its nominal Zone. That this need not be automatically the case follows from the foregoing notes in cases in which the type locality of the index species is not the same as the type locality of its nominal Zone. As we shall see below, the case of *Amm. macrocephalus* and the Macrocephalus Zone provides an excellent example.

What, then, is the current position of the Macrocephalus Zone? Systematically, after much turbulence our understanding of the species *Macrocephalites macrocephalus* has progressed to the point at which we have an unambiguous type specimen (ICZN Opinion 1275, 1984). But until now we knew neither exactly from where it came, other than that it was probably somewhere near the border of Württemberg and Bavaria; nor from what horizon it came, other than that it was the "Macrocephalen-Oolith"; nor what its biospecies as a whole looked like. Stratigraphically, to-day's residue of OPPEL's original Macrocephalus Zone had become the basal Subzone of the Lower Callovian by a process of successive elimination of the other parts by subdivision, rather than one of successively more precise stratigraphical characterization of the type horizon of the index species. The question, finally, whether *M. macrocephalus* really does occur in its modern, restricted Macrocephalus Zone and Subzone could not be answered without new evidence.

New evidence has now come to light. For the first time the type locality and type horizon of *M. macrocephalus* have been discovered. They are near the Ipf, overlooking the town of Bopfingen, within the shattered western margin of the Ries impact crater, and a famous source of fossils already in QUENSTEDT's time. Temporary sections during road-widening have yielded rich collections bed by bed, including many topotypes showing the full range of variability of the species at all stages of growth. Ancillary faunal elements belonging to other groups make it possible to correlate the faunal horizon of *M. macrocephalus* with sequences elsewhere. They show that it lies at a level somewhere already well into the Koenigi Zone. The type horizon of *M. macrocephalus* does not lie in the Macrocephalus Zone of the currently standard zonation but above it. Zonal nomenclature has therefore to be modified.

## 2. Stratigraphy of the "Macrocephalen-Oolith" at the Ipf

The Ipf lies at the northeastern end of the Swabian Alb (Fig. 1). It is a prominent outlier of thick Upper Jurassic limestones, White Jura, north of Bopfingen. The "Macrocephalen-Oolith"\*) (Fig. 2) is the highest of the subsidiary, harder

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\*) There should be no confusion between the term '-Oolith' as used in English and German texts. In German, it refers to a facies, lithology or bed, translated into English as 'oolite'. In English, it signifies the ooids themselves that make up or are scattered through the rock. The inverted commas used here to mark this distinction will be dropped in the subsequent text.



Fig. 2. Artificial outcrop of the Macrocephalen-Oolith during constructional works on the road from Bopfingen to Kirchheim am Ries in 1986. The hammer-head rests on the upper surface of bed 6.

members within the underlying, predominantly argillaceous and ferruginous Brown Jura. This weathers into more gently undulating terrain with fertile soils and there are almost no natural exposures. Exposures of the Macrocephalen-Oolith were uncommon. The area was however well known as a source of *Macrocephalites* and other ammonites since the earliest days. It was consistently referred to by QUENSTEDT and OPPEL as the "Nipf" and is the source of some other important Lower Callovian guide-fossils, including syntypes of *Amm. [Reineckeia] rehmanni* OPPEL, 1857 and the lectotype of *Amm. [Reineckeia] anceps franconicus* QUENSTEDT, 1886 (non SCHLOTHEIM, 1813).

The area was mapped in detail by ALFRED BENTZ (1924) in his doctoral dissertation. He described the stratigraphy and recorded a number of sections through the Macrocephalen-Oolith (VI–VIII, p. 39–42). These agree well with the new description given below, but his faunal lists are so brief and general that they contribute little of use to-day.

New exposures came to light in 1986 during constructional works on the road from Bopfingen to Kirchheim am Ries, along the eastern lower slopes of the Ipf. They included shallow cuttings through the whole of the Macrocephalen-Oolith which could be augmented by carefully controlled hand-excavations carried out over several days by the staff of the Stuttgarter Museum. Some 200 ammonites were collected bed by bed, the majority coming from the stratigraphically important bed 5. The preservation is often rather poor or fragmentary. Although this is due in large measure to weathering in the shallow exposures, some of it reflects a degree of reworking during sedimentation. The states of preservation and matrices are however characteristic of individual beds, and hence additional material in old collec-

tions in Stuttgart, particularly in one by the late D. SCHWARZ of Bopfingen-Oberdorf donated in 1982, could be satisfactorily assigned to its correct horizons in the section.

### 2.1. The section

The succession is shown diagrammatically in Fig. 3. The following abbreviations are used in the description of the section:

SMNS: Staatliches Museum für Naturkunde in Stuttgart;

GPIT: Geologisch-Paläontologisches Institut und Museum der Universität Tübingen.

M: macroconch, m: microconch, ammonite dimorphs.

Names in faunal lists are mostly morphospecific.

From above:

#### ? Middle Callovian

Bed 1. Ornaten-Ton: silty clays, weathered light brown, seen to ca. 0.5 m. Ammonites preserved as crushed moulds.

*Hecticoceras (Putealicerus)* sp.

Perisphinctids

#### Lower Callovian

Beds 2–7. Macrocephalen-Oolith: marly, ferruginous oolitic limestones and iron-oolitic marls in several courses. The ooliths are of variable size, unsorted, larger and darker than in the Varians-Oolith below, and concentrated in pockets by bioturbation, set in a matrix that is grey when fresh, weathering beige. Ammonites are the commonest body-fossils, preserved with shell in the limestones and as steinkerns in the marls. The total thickness of 1.35 m is greater than that recorded south and west of the Ipf (BENZ 1924). The following ammonites were obtained:

Bed 2a:

*Macrocephalites (Macr.) uhligi* LEMOINE sensu JEANNET [M]

*Homoeoplanulites (Parachoffatia)* sp. [M]

*Hecticoceras* cf. *proximum* ELMI [M]

Bed 2b:

*Macrocephalites (Macr.) uhligi* LEMOINE sensu JEANNET [M]

*Macrocephalites (Pleurocephalites)* sp. [m]

*Reineckeia* sp. [M]

Bed 3:

*Macrocephalites (Macr.) dicosmus* (GEMM.) [M]

*Keplerites (Gowericeras) indigestus* (BUCKMAN) sensu PAGE 1988 [M]

Bed 4:

*Macrocephalites (?Indocephalites) aff. sphaericus* (GREIFF-ROLLIER MS) JEANNET 1955 [M]

*Homoeoplanulites (Homoeopl.)* sp. [m]

*Oxycerites subcostarius* (OPPEL) [M]

Bed 5:

*Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M] (Pls. 1–4)

*Macrocephalites (Pleurocephalites) aff. folliformis* BUCKMAN [m] (Pl. 5, fig. 1)

= m of *Macrocephalites macrocephalus*

*Macrocephalites (?Indocephalites)* sp. [M]

*Reineckeia quenstedti* nom. nov. pro *Reineckeia franconica* (Pl. 6, fig. 1)

(QUENST., non SCHLOTH.) [M] (= *Reineckeia rehmanni* (OPPEL), subj.)

*Reineckeia grossouvrei* PETITCL. sensu CARIOU [M] (Pl. 6, fig. 2)

*Proplanulites (Propl.)* cf. *subcuneiformis* BUCKMAN [m] (Pl. 2, fig. 2)

*Proplanulites (Propl.)* cf. *fabricatus* BUCKMAN [m] (Pl. 2, fig. 3)

*Proplanulites (Crassiplanulites) basileus* BUCKMAN [M] (Pl. 9, fig. 2)

*Bullatimorphites (Kheraicerus) aff. prahecuensis* PETITCL. (Pl. 3, fig. 4)

*Bomburites (Bombur.) bombur* (OPPEL) [m]

*Chamousetia* cf. or aff. *phillipsi* CALLOMON & WRIGHT (Pl. 4, fig. 3)

(= *Amm. lenticularis* PHILLIPS, non YOUNG & BIRD) [M]

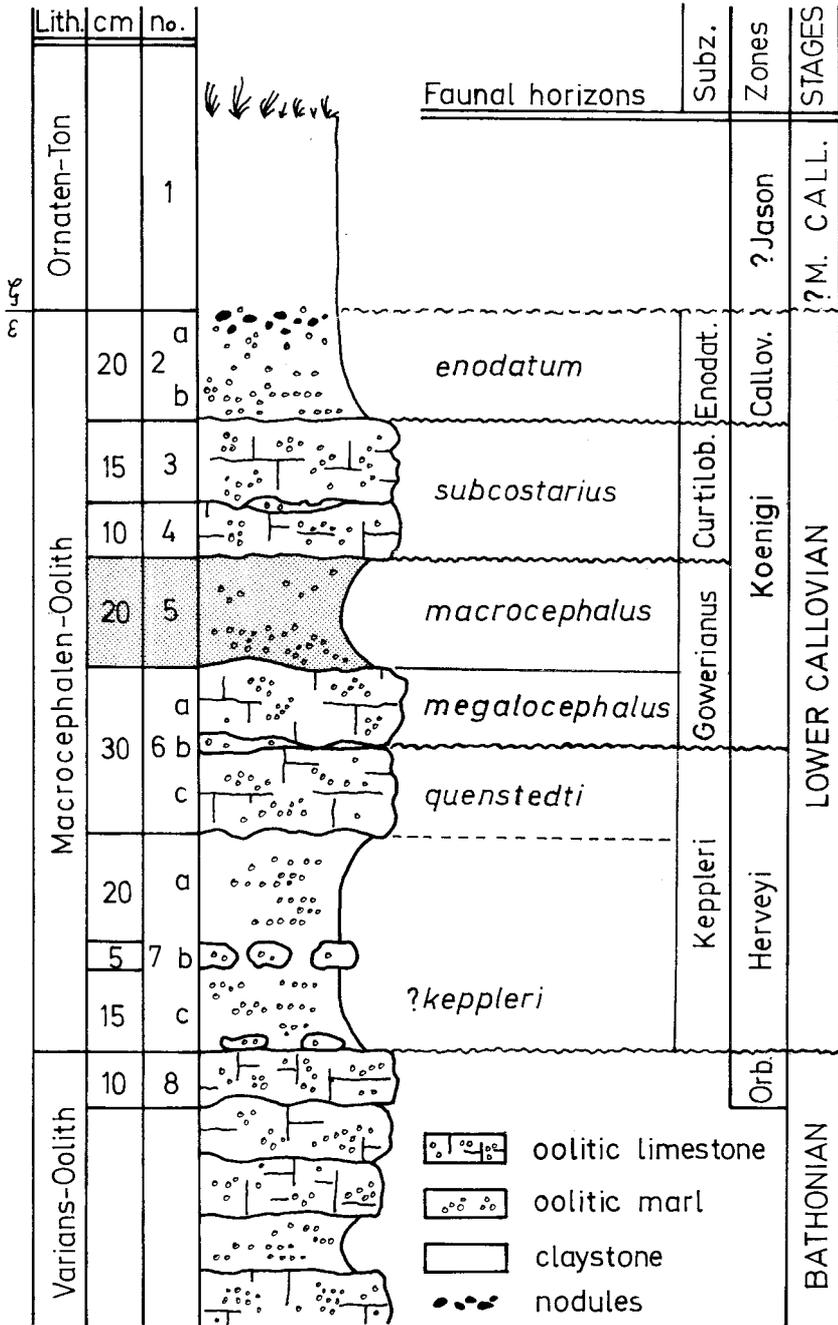


Fig. 3. Lithostratigraphy and chronostratigraphy of the "Macrocephalen-Oolith" (mainly Lower Callovian; Brown Jura epsilon). Section from the eastern slope of the Ipf between Kirchheim am Ries and Bopfingen. The bed of the *macrocephalus* horizon is shaded.

- Kepplerites (Gowericeras) densicostatus* TINTANT [M] (Pl. 7, fig. 1)  
*Homoeoplanulites (Parachoffatia) aff. funatus* (OPPEL) [M] (Pl. 5, fig. 2)  
*Homoeoplanulites (Homoeopl.) aff. furculus* (NEUMAYR) [m] (Pl. 7, fig. 2)  
*Indosphinctes (Ind.) aff. spirorbis* (NEUMAYR) [M] (Pl. 8, fig. 2)  
*Indosphinctes (Ind.)* sp. nov. [M] (Pl. 9, fig. 1)  
*Indosphinctes (Elatmites)* sp. [m]  
*Choffatia (Subgrossouvria) recuperoi* (GEMM.) [M] (Pl. 8, fig. 1)  
*Choffatia (?Grossouvria)* sp. [m]  
*Paroxycerites subdiscus* (D'ORB.) [M] (Pl. 6, fig. 3)  
*Oxycerites* sp. [M]  
*Chanasia (Jeanneticeras)* sp. [m]
- Bed 6a:
- Macrocephalites (?Indocephalites) megalcephalus* CALL., DIETL & NIEDERH. [M]  
*Kepplerites (Gowericeras) aff. metorchus* BUCKMAN [M]  
*Proplanulites (Propl.) aff. subcuneiformis* BUCKMAN [m]  
*Choffatia (Subgrossouvria)* sp. [M]  
*Indosphinctes (Ind.)* sp. [M]  
*Homoeoplanulites (Parachoffatia) funatus* (OPPEL) [M]  
*Homoeoplanulites (Homoeopl.) aff. furculus* (NEUMAYR) [m]  
*Bullatimorphites (Kheraiceras) prabecquensis* s. s. (PETITCL.) [M]
- Bed 6c:
- Cadoceras quenstedti* SPATH (coll. V. DIETZE, Aalen; cast in SMNS) [M]
- Bed 7a-c:
- Macrocephalites (Macr.) jacquoti* (H. DOUV.) [M]  
*Bullatimorphites (Kheraiceras) hannoveranus* (J. ROEM.) [M]  
*Homoeoplanulites (Parachoffatia) arkelli* MANG. [M]  
*Homoeoplanulites (Homoeopl.) homoeomorphus* BUCKMAN [m]  
*Oxycerites orbis* (GIEBEL) [M]  
 ? *Chanasia (Jeanneticeras)* sp. [m]

### Upper Bathonian

Bed 8. Varians-Oolith: limestone, marly, ferruginous, reddish brown when fresh, with fine-grained light brown ironshot ooliths.

Only the top bed of the Varians-Oolith was examined. It is sparsely fossiliferous, as elsewhere, and was not searched further for ammonites on this occasion. It had been examined previously in 1981 in yet another temporary excavation at nearby Bopfingen-Oberdorf (DIETL 1982) that exposed the whole of the Bathonian (0.75 m) and much of the Upper Bajocian, including the type horizon of *Oxycerites aspidoides* (OPPEL). The Varians-Oolith yielded *Oxycerites orbis*, confirming earlier records by BENTZ (1924) and HAHN (1968).

### 2.2. Ammonite faunal horizons

The ammonite biostratigraphy of the Lower Callovian at the Ipf has the same character as that elsewhere in the Swabian and Franconian Alb. The lithological sequence is one of sharply defined beds, sometimes very thin, often bounded by lithological discontinuities, bedding-planes or even hardgrounds that can represent considerable non-sequences, and characterized by distinguishable ammonite faunal assemblages. These assemblages cannot be stratigraphically further subdivided within a bed and may or may not show independent evidence of condensation, such as erosion, corrosion or phosphatization. Most frequently their homogeneity suggests that condensation, although probably present, was not important, i. e. that the assemblages may be treated to a good approximation as isochronous. The biostratigraphical sequence is therefore one of characteristic faunal horizons that represent the limits of time-resolution that can be achieved by means of fossils. Many of these

horizons can be followed over considerable distances and form the basis of correlation. The succession that has been pieced together in the Upper Bathonian — Lower Callovian of the southwestern and central Swabian Alb (CALLOMON, DIETL & NIEDERHÖFER 1989) is as follows. From above:

- Horizon of *Oxycerites subcostarius*
- Horizon of *Macrocephalites macrocephalus*
- Horizon of *Macrocephalites megalcephalus*
- Horizon of *Kepplerites toricellii*
- Horizon of *Macrocephalites* cf. *kamptus*
- Horizon of *Cadoceras suevicum*
- Horizon of *Cadoceras quenstedti*
- Horizon of *Kepplerites keppleri*
- Horizon of *Clydoniceras discus*
- Horizon of *Clydoniceras hollandi*
- Horizon of *Oxycerites orbis*

The ammonites collected at the Ipf indicate the following faunal horizons, in ascending order.

Bed 8 of the Varians-Oolith represents the *orbis* horizon (DIETL, 1982, Fig. 1, bed 6), much as it is developed from the Wutach, at the southwestern end of the Swabian Alb (CALLOMON et al. 1989), to Sengenthal in the Franconian Alb (DIETL & CALLOMON 1988). Its age is early Upper Bathonian, Orbis Zone.

Beds 7a–c cannot at present be unequivocally assigned on the basis of the limited material available. All the specimens found could as well have come from the Upper Bathonian Discus Zone as from the basal Callovian *keppleri* horizon. To distinguish these would need either some of the diagnostic but relatively rare forms such as *Kepplerites* or *Clydoniceras*, or more abundant assemblages of e.g. the perisphinctids that would then differ in ranges of morphological variability. Regional experience strongly suggests, however, that bed 7 represents the *keppleri* horizon. The *hollandi* horizon has so far been clearly characterized only in the Wutach area (CALLOMON et al. 1989). Indications of the presence of a *discus* horizon have been known for some time in the region of the Zollernalb in the central Swabian Alb (cf. RIEBER 1961, DIETL 1982, p. 12), and its presumed position there at the top of the Orbis-Oolith (formerly *Aspidoides*-Oolith), immediately below the *keppleri* horizon, has been confirmed (to be published). But its development is also only very local. In contrast, the *keppleri* horizon has been widely recognized, from Liesberg in the Jura Bernois, via its type area near Balingen, the type area of *K. keppleri* near Reutlingen, as far as Sengenthal in Franconia. We assume therefore that bed 7 does represent the *keppleri* horizon and that the absence of the index-species is due to collection failure.

Bed 6c is firmly assigned to the *quenstedti* horizon. The *Cadoceras* from it is unmistakable.

Bed 6b, which is little more than a marly parting that has yielded no ammonites, marks a major non-sequence spanning at least the three horizons falling into it further south.

Bed 6a is assignable to the *megalcephalus* horizon (index *Macrocephalites megalcephalus* nom. nov. CALL., DIETL & NIEDERH. 1989 pro *Amm. macrocephalus rotundus* QUENSTEDT, 1846, non SOWERBY 1821; including QUENSTEDT 1886, pl. 76, fig. 13, from the Ipf). It is indicated by the large *Macrocephalites*, and the true *Bullatimorphites praehacquensis* associated with an early *Proplanulites*.

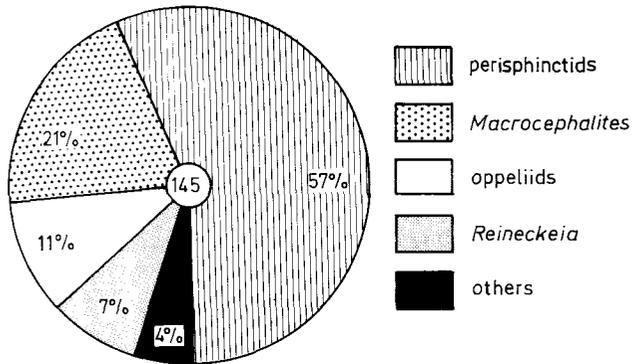


Fig. 4. Diagram of ammonite distribution within bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen.

Bed 5, the *macrocephalus* horizon, is the most fossiliferous bed in the section. A count of the identifiable specimens gives the following composition:

Pseudoperisphinctinae	<i>Choffatia</i> etc.	80
Macrocephalitinae	<i>Macrocephalites</i>	56
Oppeliinae	<i>Oxyerites</i> etc.	15
Reineckeiidae	<i>Reineckeia</i>	10
Tulitidae	<i>Bullatimorphites</i>	2
Kosmoceratidae	<i>Keplerites</i>	3
Proplanulitidae	<i>Proplanulites</i>	1
Cadoceratidae	<i>Chamoussetia</i>	1

This is shown diagrammatically in Fig. 4. The fauna is predominantly Submediterranean in character, but the minority of Subboreal elements is of great importance for correlation. The morphological variabilities within each of the two abundant sub-families smoothly intergrade and the assemblage of *Macrocephalites* contains almost no variants also known from other previously characterized Swabian faunal horizons. The conclusion is that although some condensation cannot be ruled out – it hardly ever can – it is here effectively not important and the assemblage characterizes an individual faunal horizon previously unrecognized in the Swabo-Franconian Lower Callovian. It was already briefly described in a previous review (CALLOMON, DIETL & NIEDERHÖFER 1989: 10). But its greatest interest lies in that it is without doubt the type horizon of *Amm. macrocephalus* SCHLOTHEIM as represented by the neotype (CALLOMON 1971). It has yielded specimens that agree with the neotype in minute detail (see Pl. 1), both in morphology and the rather characteristic lithology and preservation. The species can now be fully characterized and is described in the systematic section below. The consequences for stratigraphical nomenclature are also discussed. It is one of the ironies of history that the precise horizon of one of the earliest index-species in standard stratigraphy should have been one of the last to be discovered.

Beds 3–4 together represent the *subcostarius* horizon. Its faunas are currently under closer study in the southwestern Alb, around Geisingen and Blumberg-Zollhaus where it is particularly well developed (NIEDERHÖFER, in prep.). The diagnostic elements found at the Ipf are *Keplerites indigestus* sensu PAGE (1988), *Oxyerites subcostarius* (OPPEL) and *Macrocephalites dicosmus* (GEMMELLARO, 1873: holotype

Pl. 2, fig. 5), relatively abundant, a macroconch probably closely related to, if not exactly coupled with, *Macrocephalites gracilis* (SPATH), a microconch, index of the Submediterranean Gracilis Zone.

Bed 2 represents the *enodatum* horizon. The ammonite fauna of this horizon is not very rich. *Macrocephalites uhligi* LEMOINE sensu JEANNET and *Hecticoceras* cf. *proximum* ELMI indicate the Enodatum Subzone of the Calloviense Zone.

Bed 1 is the lowest member of the Ornatenton, of which only the basal part was preserved in the sections. A sharp lithological break is accompanied by an abrupt change in the ammonite faunas. *Hecticoceras* (*Putealicerias*) indicates the Middle Callovian, but the limited and poorly preserved material rules out more precise assignments.

### 2.3. Ages and correlations

The standard chronostratigraphy of the Lower Callovian has recently been revised. Faunal provincialism of the ammonites leads to the recognition of two major faunal provinces in Europe. Their faunal successions are so different that each has to be given its own separate standard zonal classification. The Subboreal Province is typified by Britain, Normandy and northern Germany and extends eastwards through Poland as far as Trans-Caspia and the northern Caucasus. The Submediterranean Province is typified by the Aquitaine and Rhodanean Basins of western and southern France (CARIOU 1984, 1985) and includes Spain, Sicily, Hungary and the Balkans. The position of Franconia, Swabia and the northern Jura is intermediate, in the region of provincial overlap, tending in its affinities now more to the one, now more to the other of the two provinces. In deciding which standard zonation to adopt, what matters is the precision with which faunal horizons can be correlated with the standards. For this purpose some elements of the faunas are often much more important than others, irrespective of their relative abundances. This has turned out to be the case in the Swabian Callovian, and the standard zonation chosen is that of the Subboreal Province despite the fact that the major proportion of the ammonites at almost all levels is submediterranean in character.

The currently standard chronostratigraphy of the subboreal Lower Callovian is shown in Fig. 5 (chapter 3 below) and the zonal and subzonal assignments of the succession at the Ipfl are included in Fig. 3. The only horizon whose correlation calls for comment here is the previously unrecognized *macrocephalus* horizon, bed 5. The evidence from Swabia establishes only its relative position; above the *megaloccephalus* horizon and below the *subcostarius* horizon.

The correlation of the *megaloccephalus* horizon with some level in the Koenigi Zone of the Subboreal standard is based on the occurrence in it in Swabia of *Proplanulites* and *Keplerites* (*Gowericeras*) aff. *metorchus*. In Britain the abrupt first occurrence together of *Proplanulites* and *Keplerites* (*Gowericeras*) characterizes the base of the Koenigi Zone. In Swabia, the *megaloccephalus* horizon lies either immediately above a non-sequence or above the *toricelli* horizon which contains the earliest Swabian *Keplerites* (*Gowericeras*). The species of *Gowericeras* found in the *megaloccephalus* horizon is not identical with the earliest English species (*Gow. metorchus*). *Keplerites* (*Gowericeras*) *gowerianus* is also very close. It is not certain, therefore, whether the *megaloccephalus* horizon lies at exactly the level of the first occurrence of *Keplerites* (*Gowericeras*) in Britain, but it cannot be far off. Correlation with the Submediterranean standard depends on the occurrence of *Bullatimor-*

*phites prahecquensis* (PETITCLERC). In western France this marks the *prahecquensis* horizon, the higher of only two horizons so far distinguished there in the lowest, Bullatus Zone.

Correlation of the *subcostarius* horizon with the Subboreal standard is somewhat more tenuous. Indirectly, the *subcostarius* horizon of Swabia has elements in common with the *laugieri* horizon of western France, which has been correlated with the lower Calloviense Zone (CARIOU, 1985). But the *Kepplerites* (*Gowericeras*) *indigestus* from the Ipf indicates the upper Curtilibus Subzone of the Koenigi Zone directly. This suggests still the Koenigi Zone. Together, therefore, the evidence of the faunal horizons below and above it place the *macrocephalus* horizon firmly somewhere in the Koenigi Zone.

Direct evidence comes from the fauna of bed 5 itself. The *Kepplerites* (*Gowericeras*) *densicostatus* in it is characteristic of a faunal horizon well known from Poix in the Ardennes (CORROY, 1932: 32). The *Kepplerites* from this locality were figured by TINTANT (1963, pls. 12, 13, 15). They constitute a homogeneous assemblage that is close to, but differs consistently in details of coiling and sculpture from, those both of *Kepplerites* (*Gowericeras*) *metorchus* BUCKMAN and *Kepplerites* (*Gowericeras*) *gowerianus* (SOWERBY), which occur in horizons VIII and IX of the British Gowerianus Subzone respectively (CALLOMON, DIETL & PAGE 1989 and CALLOMON, DIETL & NIEDERHÖFER 1989, tab. 1, p. 6 – “XIII“, in error). One of them (TINTANT, pl. 15, figs. 1a, b) was made type of a new subspecies *Kepplerites* (*Gowericeras*) *gowerianus densicostatus*, and if we interpret this in the sense of chronosubspecies, or transient, of *Gowericeras*, the name may be used to label the faunal assemblage as a whole and its horizon as the *densicostatus* horizon. The specimens from the *macrocephalus* horizon of the Ipf fall most readily into the range of variability of *Kepplerites* (*Gowericeras*) *densicostatus*, suggesting that the two horizons are very close in age, even if not identical.

The numerous *Proplanulites* from Poix figured by CORROY match those of horizons VIII and IX (CALLOMON et al. 1989: tab. 1; PAGE 1990) of the Gowerianus Subzone exactly. So do the specimens from the Ipf, although not much weight should be put on this. Similarly, some of the early forms of *Indosphinctes* from the Ipf can be matched with forms from Poix. Both the *macrocephalus* horizon at the Ipf and the *densicostatus* fauna have also yielded each a *Chamoussetia*. A recent revision of this genus in Britain has shown that it occurs there at two distinct levels. The form from Poix (CORROY, pl. 11, figs. 3, 4) matches the English forms from the lower level, which is immediately above the main level of the *metorchus* horizon, lower Gowerianus Subzone in England. The form from the Ipf is too small to identify closely (see chapter 4 below) and could be from either level, or inbetween.

Finally, *Macrocephalites* itself. This genus is relatively common in the English lower Koenigi Zone at one as yet not closely identified level in the beds collectively placed in the *metorchus* horizon. The fauna at this level consists of *Macrocephalites* (*Pleurocephalites*) *lophopleurus* BUCKMAN (including *folliformis* BUCKMAN, *liberalis* BUCKMAN and numerous other variants). The problem is that the English material consists almost wholly of microconchs (as do the specimens known from Poix), whereas the Swabian collections are made up predominantly of macroconchs. Close comparisons are therefore difficult. Although doubtlessly fairly close to *M. macrocephalus*, there are consistent and significant differences. English *Pleurocephalites* are similarly close to but distinct from the microconchs of the *megalocephalus* horizon.

Other than at this *lophopleurus* level, *Macrocephalites* is rare in the Koenigi Zone in Britain. One specimen has however been found (K. N. PAGE coll.) that seems truly to belong to *M. macrocephalus* (see below). It came from a concretion in beds assigned to the *gowerianus* horizon.

In summary, the position of the *macrocephalus* horizon is firmly in the Koenigi Zone, almost certainly still in the Gowerianus Subzone, and then most probably in the upper part.

Elsewhere in Swabia the *macrocephalus* horizon has yet to be firmly identified. There are indications of its presence in the Wutach area in the form of occasional specimens very close to *M. macrocephalus* in old collections, notably that of SCHALCH in Schaffhausen. Its presence in Lower Saxony has recently been reported by E. MÖNNIG (1989, p. 105; Ziegelei Temme, Hildesheim, old pit, bed 4, p. 63; ? new pit, bed 9, p. 69). Unfortunately it is represented there by only a layer of more or less remanié concretions immediately below a major non-sequence leading straight into the Jason Zone and adds nothing to general correlations.

### 3. The nomenclature of the Macrocephalus Zone

The evolution of the zonal classification of the Lower Callovian Substage is summarized in Fig. 5.

#### 3.1. OPPEL'S Zonation and his Zone of *Ammonites macrocephalus*

D'ORBIGNY'S "6<sup>e</sup>. Étage Callovien" (1850, p. 608) was first subdivided by OPPEL (1857, p. 503). He divided it into three Zones: the Zone of *Amm. athleta* (upper), the Zone of *Amm. anceps* (middle), and the Zone of *Amm. macrocephalus* (lower part of the Callovian Stage).

There has been much debate as to the exact meaning of OPPEL'S "Zones", but there can no longer be much doubt that they were what to-day we call standard chronozones, that this is what they were meant to be from the beginning, and that it is what most authors have always taken them to be, even if not in so many words. The indications are after all quite clear already in OPPEL'S own text and tables. Jurassic rocks are classified according to their ages, irrespective of their lithologies etc. Stages are continuous, serial subdivisions of the Jurassic System ("Juraformation"), without gaps or overlaps. Zones are similarly subdivisions of Stages, and Stages are groupings of Zones. Every piece of rock therefore belongs uniquely to one or other Zone, even if in practice we cannot always determine which; and the boundaries between Zones are therefore time-planes – which is what the horizontal lines in any of the innumerable tables of zonal classifications that have been published signify, including OPPEL'S. Where the boundaries should be drawn was determined by the fossils in the rocks – their biostratigraphies – in such ways that would optimize the ability to recognize the Zones as widely as possible. The primary task was the identification of those fossils that were reliable zonal indicators, as opposed to those that were not. They are the guide fossils, and their enumeration takes up a large part of OPPEL'S book.

To be able to recognize a Zone as widely as possible it is obviously desirable not to have to rely on the presence or absence of a single guide-fossil, but to have recourse to any of a whole group of guide-fossils. OPPEL'S Zones were therefore based on assemblages of characteristic fossils, which he listed. All they had in common was

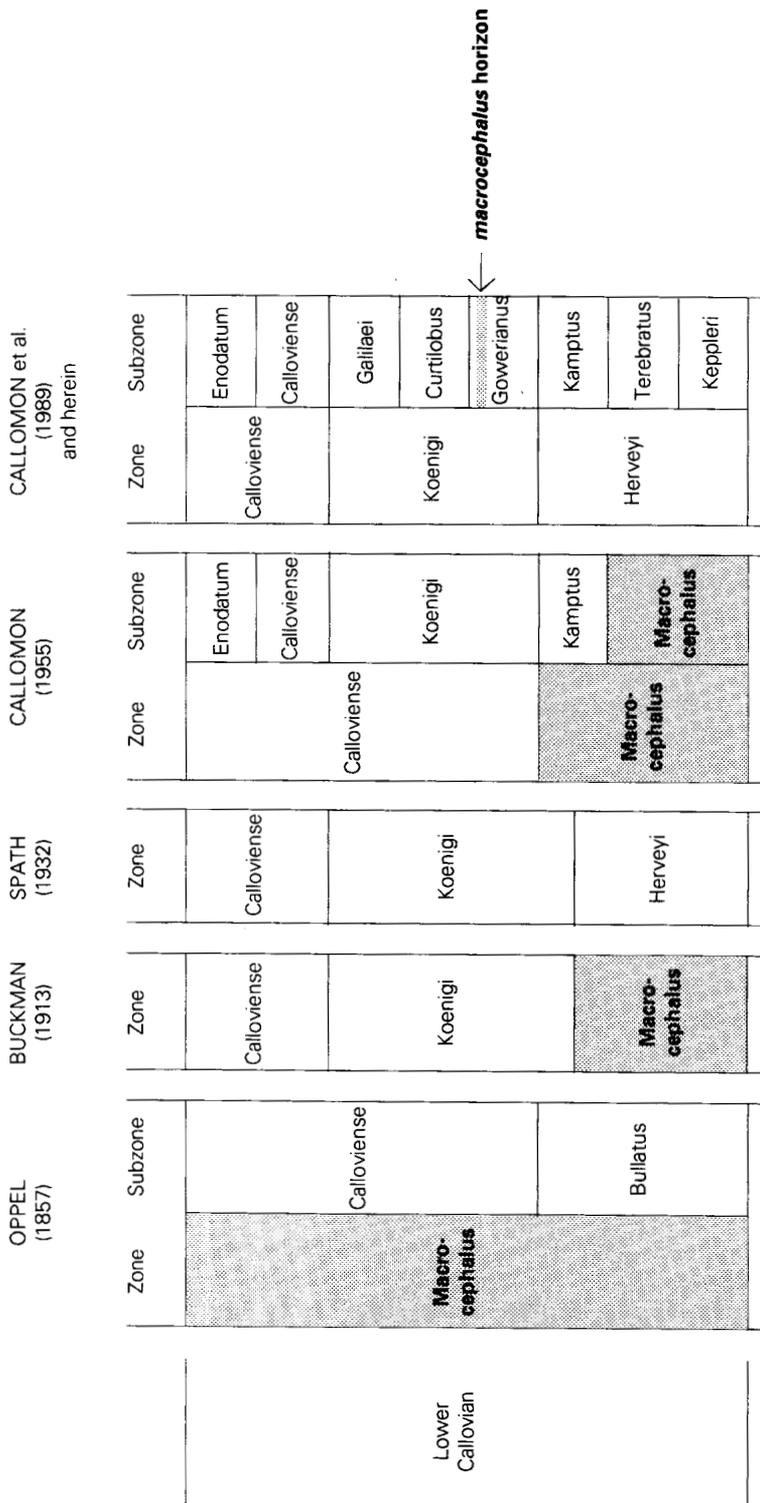


Fig. 5. The currently standard chronozonation of the subboreal Lower Callovian in comparison with older zonal classifications.

that, to the best of OPPEL's knowledge, they occurred within those of his Zones for which he listed them. This did not imply that the limits of the ranges of all the species in a characteristic zonal assemblage had to coincide with the zonal boundaries, that these boundaries had to represent what to-day we call horizons of first and last appearances. Known ranges change all the time, and no-one more than OPPEL himself regretted the limitations put on his ability to correlate formations by the incomplete state of knowledge of the ranges of species.

Nomenclature: just as the Stages, so the Zones have to be given names. OPPEL decided to retain D'ORBIGNY's convention of naming Stages after places. For cogent reasons (p. 813), he decided after considering the alternatives to name his Zones each after "one of its more important species" of guide-fossils. But he did not explain what he meant by "important", and this has been the major cause of subsequent confusion. As knowledge grew of the ranges of individual species, both stratigraphical and geographical, so one species became more "important" than another, and authors felt compelled to modify their zonal classifications accordingly. In the limit, stratigraphical classification became that of single-species range biozones, which is subjective, depending on the zoological interpretation of the species, and varies from place to place, depending on facies and biogeography. Such a classification defeats the whole purpose of OPPEL's work, which was to provide a permanent regional standard. He himself stressed that the sole function of the species selected to name the Zones was nomenclatorial. To-day we express this function by distinguishing between the use of species as guide-fossils and as index-species.

A zonal index-species should be a member of the characteristic assemblage of zonal guide-fossils, i. e. occur in its nominal Zone, but need be neither the commonest member nor the most widely used in correlation, as the examples discussed above, in the *megalocephalus* and *macrocephalus* horizons, illustrate. How often is *Gregoryceras transversarium* used to recognize OPPEL's Transversarium Zone? Although a reliable guide-fossil, it is also one of the rarest in the assemblage. But it is certainly the most striking, the most easily identified.

Given this restricted function, there can be only two reasons for changing the index species of a standard Zone. The first is that the species has been misidentified. A recent example (DIETL 1982) is that of *Oxycerites aspidoides* (OPPEL), index of the Upper Bathonian Aspidoides Zone, which had been confused with homoeomorphic *Oxycerites orbis* (GIEBEL). The second is that the index species, although correctly identified, does not occur in what to-day is the Zone named after it. This has now been found to be the case in the Macrocephalus Zone.

### 3.2. The Macrocephalus Zone in a restricted sense

The zonal classification of the Callovian has evolved by subdivision. OPPEL's Macrocephalus Zone as a whole has become synonymous with the Lower Callovian Substage. The first to discern the possibility of further subdivision was OPPEL himself. He had noticed during his travels in England that the upper part of the beds that he had, correctly, put as the equivalents of the "Schichten des *Amm. macrocephalus*" in Swabia contained ammonites not known in Swabia, including *Amm. calloviensis*, and that vice versa the Macrocephalus-Schichten of Swabia contained some unknown in England, including *Amm. bullatus*. He therefore tentatively referred to a possible two-fold subdivision of the Zone of *Amm. macrocephalus* into Subzones (p. 504) or Horizons (*sic*, p. 507), of *Amm. bullatus* below and *Amm. calloviensis*

above. OPPEL has therefore always been regarded as the author of the Bullatus and Calloviense Zones or Subzones despite the hesitant manner in which he introduced the terms.

The Calloviense Zone was soon firmly adopted in England for the Kellaway Beds, i. e. the upper part of OPPEL's Macrocephalus Zone, by WRIGHT (1872, p. 207), one of the leading Jurassic stratigraphers of the time. He was followed in a comprehensive and authoritative review of the whole of the Jurassic rocks of Britain by WOODWARD (1894, p. 434; 1895, p. 8). The lower part of the original Macrocephalus Zone, represented by part of the Cornbrash, was however not assigned to the Bullatus Zone. The index, *Amm. bullatus*, was (and continues to be) unknown in Britain. Instead, the name Macrocephalus Zone was retained, now in a restricted sense. It certainly yielded *Macrocephalites*, including forms identified at the time as *M. macrocephalus*. The absence of *Amm. bullatus* in Britain and the rarity or absence of *Amm. calloviensis* in southern France are now known to reflect bioprovincial segregation. That the first attempts at zonal refinement of the Lower Callovian were made in Subboreal Britain rather than in Submediterranean France was a historical accident. The Bullatus Subzone was revived as soon as a modern revision of the French Lower Callovian began (CARIOU, ELMI, MANGOLD, THIERRY & TINTANT 1971) and is currently the lowest member of the Submediterranean standard Callovian zonation.

Fig. 5 charts the subsequent history of the Subboreal Lower Callovian. The Koenigi Zone was introduced by BUCKMAN (1913) who retained the Macrocephalus Zone but in an even more restricted sense than that in which WRIGHT had left it. SPATH (1932: 145), in a description of the Bathonian-Callovian deposits of East Greenland, gave without further explanations a summary table of correlations against a zonal scale which is an inconsistent hybrid of old and new. The only noteworthy feature was the appearance of a Herveyi Zone with the same meaning as the restricted Macrocephalus Zone of Buckman. The Macrocephalus Zone was still alluded to in a re-expanded sense, to include both the Koenigi and Herveyi Zones; but whereas the Koenigi Zone was in the Callovian, the Herveyi Zone was placed still in the Bathonian.

New stratigraphic evidence in Britain led to the first comprehensive review (CALLOMON 1955, 1964) of the Lower Callovian since those of BUCKMAN and WRIGHT, which were taken as the starting-point. Additional subdivisions were introduced, but at Subzonal rank. There resulted finally a Macrocephalus Subzone as the basal Subzone of the Callovian, the residue in its most restricted sense of OPPEL's original Macrocephalus Zone.

This was the final product of a process of contraction by elimination based on new stratigraphical evidence. The Macrocephalus Subzone represented simply what was left as the least understood, unrevised part of the British Lower Callovian. In Britain, the ammonites of the Cornbrash were known essentially only from specimens in the museums (BLAKE 1905). Even a detailed biostratigraphic revision by ARKELL served only to establish that *Macrocephalites* was restricted to the highly condensed Upper Cornbrash (DOUGLAS & ARKELL 1928, 1932, 1935; ARKELL 1954). It produced no significant new material. In Swabia, there had been no biostratigraphical progress in the Lower Callovian since QUENSTEDT's time: Varians-Schichten, followed by Macrocephalen-Oolith with *Macrocephalites*, overlain by Ornatenton. The Macrocephalen-Oolith represented the Macrocephalus Zone sensu OPPEL and, in the absence of

any more detailed systematic treatment of the genus *Macrocephalites*, had to include the type horizon of the index species, *M. macrocephalus*, no matter how this species might be interpreted.

### 3.3. The *Macrocephalus* Zone renamed: the *Herveyi* Zone

The previous section has outlined the history of the stratigraphy. It is self-consistent and independent of the history of the index species, *M. macrocephalus*. The stratigraphic classification had reached almost its final stage in 1955, despite the fact that at that time no-one knew what the species *M. macrocephalus* was, there being no type specimen, and hence even less as to where in OPPEL's original *Macrocephalus* Zone, now the Lower Callovian, the type horizon of the species lies.

The problem of the systematic interpretation of *Ammonites macrocephalus* SCHLOTHEIM, 1813, was solved later (CALLOMON 1971), with the designation of a neotype specimen (see below, chapter 4). The arguments had to be based on the principles of zoological classification in accordance with the Code of Zoological Nomenclature, not on stratigraphy. The specimen chosen was one of SCHLOTHEIM's former syntypes and all that was known about its origin was that it came from "dem Öttingischen", somewhere near the Württemberg-Bavarian border. Both the most probable type locality and certainly the type horizon have now been discovered. The type horizon lies not in the *Macrocephalus* Zone in the restricted sense but in the *Koenigi* Zone above. This is clearly a case falling into one of the categories cited above, and it becomes necessary to find an alternative index species for the *Macrocephalus* Zone. The proposed new index is *Macrocephalites herveyi* (J. SOWERBY, 1818), and the Zone becomes the *Herveyi* Zone.

The principal reason behind this choice is historical. It revives the first alternative choice of index proposed by SPATH in 1932, which, apart from *Amm. bullatus*, is also the only alternative ever to have been proposed. The name of the species, *Amm. herveyi*, is well known and deeply rooted in the literature, being cited and illustrated already by ZIETEN (1831), D'ORBIGNY (1846, p. 428, pl. 150 [= *Amm. grantanus* OPPEL, 1857]; 1852) and OPPEL himself (1857 p. 507, 548) who had probably seen the types in London. The precise interpretation, however, was almost as uncertain as that of *Amm. macrocephalus* for similar reasons.

The species *Amm. herveyi* was based on two syntypes (J. SOWERBY 1818, p. 215, Pl. cxcv, two figures), neither of which has ever been refigured since. The larger syntype was designated lectotype by SPATH (1928, legend to Pl. 43, fig. 2a, b, which is an illustration of the septal suture). The smaller syntype became type of a new species *Kamptokephalites subpila* SPATH (1928, p. 173). The lectotype is now refigured here in Fig. 6 and 7. It is a complete microconch with the coarse biplicate ribbing characteristic of the group commonly called *Kamptokephalites*. It came from the Cornbrash of an unknown locality in eastern England, most probably around Bourne in Lincolnshire, about 30 km north of Peterborough. Specimens like it are rare, but this would be understandable if the type were merely an extreme variant of the relatively common group of *Kamptokephalites* that includes *K. kamptus* itself, a more typical variant. Specimens very close to the type are known from a number of localities from Peterborough northwards, as far as the Yorkshire coast. None of these has been collected in situ either, but together they indicate a horizon in the lower part of the *Kamptus* Subzone. The index species is therefore not a good guide fossil, but few species of *Macrocephalites* are. It does however occur squarely in its nominal Zone,

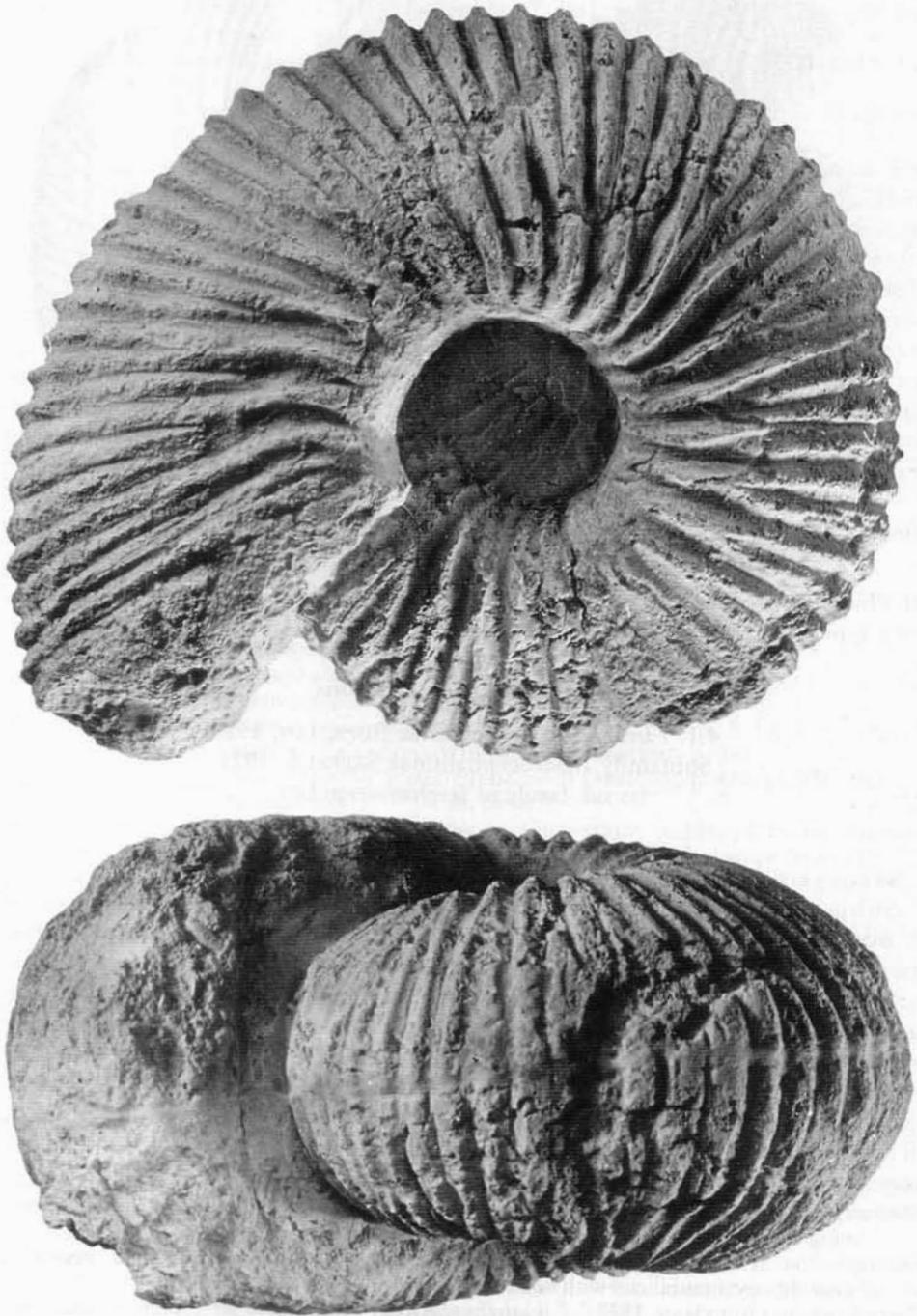


Fig. 6. Lectotype of *Macrocephalites herveyi* (J. SOWERBY). - x1.

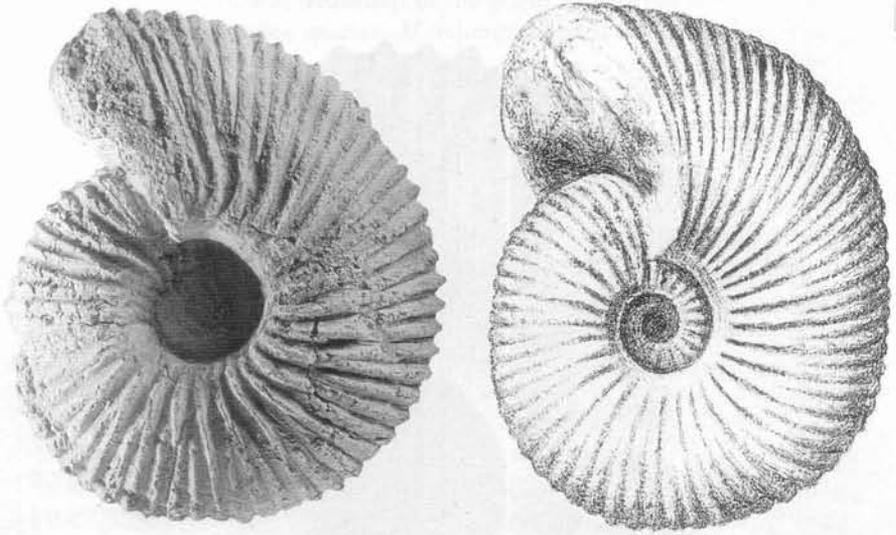


Fig. 7. Lectotype of *Kamptokephalites herveyi* (J. SOW.) compared with SOWERBY'S figure. — x1/2.

of which the group of *Kamptokephalites* as a whole to which it belongs is certainly very typical and widely recognizable, in both northern and southern hemispheres.

#### 4. Systematic descriptions

- 4.1. Family Sphaeroceratidae BUCKMAN, 1920  
 Subfamily Macrocephalitinae SALFELD, 1921  
 (as sub-family of Stephanoceratidae)

##### Genus *Macrocephalites* ZITTEL, 1884

Synonyms: *Macrocephalicerus* BUCKMAN, 1922 (obj.).

Subgenera. — Attempts for over a century to subdivide the "Macrocephali" of v. BUCH further on the basis of some systematically recognizable features of their morphologies had little success. The easily apprehensible characters of whorl-inflation, size, strength of ribbing and density of ribbing seemed to occur in all combinations. Nevertheless, a number of what appeared to be distinct types of morphology were picked out and given separate generic names. These have received wide currency in the literature, sometimes as wholly separate genera, but more often as subgenera of *Macrocephalites*. The subsequent diagnosis of dimorphism in this group, as in so many others, allows these taxa now to be classified into macro- [M] and microconchs [m]. They may be briefly reviewed as follows:

- Macrocephalites* ZITTEL, 1884 s. s. (\**Amm. macrocephalus*); [M], large, densely ribbed, becoming smooth; relatively small, steep-sided umbilicus.  
*Indocephalites* SPATH, 1928 (\**I. kheraensis*); [M], like *M.* s. s., large, inflated, becoming smooth; open umbilicus with rounded margins.  
*Tmetocephalites* BUCKMAN, 1923 (\**T. bathytmetus*); [M], medium to large, compressed, involute, densely but strongly ribbed on inner whorls, becoming smooth.  
*Nothocephalites* SPATH, 1928 (\**N. asaphus*); [M], small, compressed, very fine-ribbed, becoming smooth.

*Kamptokephalites* BUCKMAN, 1922 (\**K. kamptus*); [m], moderately involute and inflated; very coarse, mainly biplicate ribbing to the end.

*Pleurocephalites* BUCKMAN, 1922 (\**P. lophopleurus*); [m], evolute, inflated; densely but strongly ribbed to the end.

*Dolikephalites* BUCKMAN, 1923 (\**D. dolius*); [m], involute, compressed; densely ribbed to the end.

Type species: *Ammonites macrocephalus* SCHLOTHEIM, 1813, subsequently designated by LEMOINE 1910 (p. 15); ICZN Opinion 1275.

Ages and distribution. — Middle Bathonian — early Middle Callovian. The earliest forms are known from the SW Pacific, in Indonesia and New Guinea. They were described by BOEHM (1912) and have recently been revised with new stratigraphical information (WESTERMANN & CALLOMON 1988). They first appeared as rare immigrants in Europe in the Orbis Zone of the Upper Bathonian (DIETL 1981; DIETL & CALLOMON 1988). They then flooded over the whole of the Tethys at the base of the Callovian, from Portugal to the Caucasus on the northern side, to Kenya, Madagascar, Cutch and Nepal in the south. *Macrocephalites* apparently did not reach the Eastern Pacific (the American Cordillera), where its place is taken by a parallel lineage, the Eurycephalitinae, derived from the same root in *Sphaeroceras*. The youngest forms known so far occur in the Medea Subzone of the Jason Zone, earliest Middle Callovian, in Europe.

*Macrocephalites macrocephalus* (SCHLOTHEIM)

Pl. 1, fig. 1; pl. 2, fig. 1; pl. 3, figs. 1–3; pl. 4, figs. 1, 2;

pl. 5, fig. 1; text-figs. 8, 11, 12; table 1.

- 1757 *Cornu Ammonis opere foliaceo signatum*. — BAIER, p. 18, pl. 12, fig. 8.
- \* 1813 *Ammonites macrocephalus* SCHLOTHEIM, p. 70.
- 1820 *Ammonites macrocephalus*. — SCHLOTHEIM, p. 70.
- aff. 1830 *Ammonites macrocephalus* SCHLOTHEIM. — ZIETEN, p. 6, pl. 5, fig. 1.
- aff. 1843 *Ammonites macrocephalus* SCHLOTHEIM. — QUENSTEDT, p. 363.
- non 1846 *Ammonites macrocephalus* SCHLOTHEIM. — D'ORBIGNY, p. 430, pl. 151, figs 1, 2 ("variété comprimée"). — [= *M. verus*?]
- non 1847 *Ammonites macrocephalus rotundus*. — QUENSTEDT, p. 184, pl. 15, fig. 2a, b. — [= *Macr. megalcephalus* CALL., DIETL & NIEDERH., holotype (mon.)]
- non 1847 *Ammonites macrocephalus rotundus*. — QUENSTEDT, p. 184, pl. 15, fig. 2a, b. — [= *Macr. megalcephalus* CALL., DIETL & NIEDERH., holotype (mon.)]
- non 1884 *Macrocephalites macrocephalus* (SCHLOTHEIM). — ZITTEL, p. 470, fig. 655. — [= *M. verus*, neotype]
- 1887 *Ammonites macrocephalus rotundus*. — QUENSTEDT, p. 651, pl. 76, fig. 13.
- non 1900 *Macrocephalites macrocephalus* (SCHLOTHEIM). — HYATT, in ZITTEL-EASTMAN, p. 580, fig. 1209. — [D'ORBIGNY's figure of 1846 reproduced, quoted as from "Ehningen, Württemberg"]
- cf. 1905 *Macrocephalites macrocephalus* SCHLOTHEIM. — BLAKE, p. 43, non p. 44 et seq., nec figs. — [Designation of BAIER's specimen as type of SCHLOTHEIM's species]
- non 1922 *Macrocephalicerias macrocephalum* (SCHLOTHEIM). — BUCKMAN, pl. 313. — [Type species of new genus]
- non 1922 *Macrocephalites verus* BUCKMAN, pl. 324A, B. — [Specimen ex OPPEL coll. believed to have been the basis for ZITTEL's figure of 1884; holotype, now lost]
- 1924 *Macrocephalites macrocephalus* (SCHLOTHEIM). — BENTZ partim, p. 18, 39.
- non 1929 *Macrocephalites macrocephalus* ZITTEL. — BUCKMAN, pp. 2, 5.
- 1971 *Macrocephalites macrocephalus* (SCHLOTHEIM). — CALLOMON, p. 119, text-fig. 2a, pls. 15, 16. — [Neotype designated and described]
- non 1971 *Macrocephalites macrocephalus* ZITTEL (non SCHLOTHEIM). — CALLOMON, p. 125, text-fig. 3, pl. 17, pl. 18, fig. 1. — [ZITTEL's specimen of 1884 rediscovered and described; neotype of *M. verus* BUCKMAN]

- non 1978 *Macrocephalites macrocephalus macrocephalus* (SCHLOTHEIM) sensu ZITTEL 1884. — THIERRY, p. 152, 203 et seq. — [Pl. 8, fig. 1a, b = ZITTEL's specimen refigured; *Amm. macrocephalus* SCHLOTHEIM excluded from *Macrocephalites*!]
- 1980 *Macrocephalites macrocephalus* (SCHLOTHEIM). — CALLOMON, p. 109. — [Application to ICZN to ratify neotype proposed in 1971; confirmed in Opinion 1275, March 1984]

Type specimen. — When founding the species, SCHLOTHEIM referred to only one specimen, the one figured by BAIER. According to the Rules (International Code of Zoological Nomenclature, Art. 72), this does not automatically make it the holotype. The type series includes all the specimens the author regarded as belonging to the species when founding it, whether he referred to them or not. In many species founded in the early days of palaeontology, little stress was placed on the selection of type specimens; and type-series often contained many specimens in the collections of the author or of his friends that were not expressly mentioned. SCHLOTHEIM himself was a keen collector and it seems highly unlikely that he would have introduced a new and so aptly named species on the basis of a single, poor illustration in the literature. In fact, in 1820 he refers to 12 specimens in his collection, some of which, even if not all, must already have been in his collection in 1813. When his collection arrived at the Humboldt University in Berlin in 1833 it contained more than 35 specimens, registered as *Amm. macrocephalus* in a catalogue compiled by QUENSTEDT who was the newly-appointed custodian at the time (1888, p. 1102). This catalogue still exists today. BLAKE (1905), in discussing the absence of further information in SCHLOTHEIM's publication of 1813, referred to BAIER's figure, stating that "This, therefore, must be taken as the type of *Macrocephalites macrocephalus*" — a clear lectotype designation.

Unfortunately, BAIER's lectotype has long been lost. His figure is, moreover, essentially uninterpretable beyond portraying an inflated, round-whorled ammonite that could well have been a *Macrocephalites*. Details of locality or horizon there were none. Interpretations of *Amm. macrocephalites* began subsequently to diverge, and the subsequent history (see below) provides a classical example of the confusion that can arise in systematic palaeontology when a species has no unique type specimen. In zoology, a type specimen can never represent a biological species completely, incorporating all its typical morphological features, including their variability. But even the incomplete representation by a type specimen can serve to exclude specimens that are thought not to belong to it and thereby to differentiate the species from others. In palaeontology a type specimen fulfills a second very important function: it defines the type horizon of a chronospecies. Failure to take this into account provides a further source of confusion, also amply illustrated in the present example. When the holotype of a species, if it had one, or the lectotype if it did not, has been lost, it becomes necessary to select a neotype. This should, if possible, be a topotype — a specimen from the same locality and horizon as those of the lost type. If these are not known, as in the present case, the choice of a specimen as neotype should be supported by detailed arguments showing that it approaches what was known of the lost type as closely as possible. After two abortive attempts, one by BUCKMAN (1922), the other by ARKELL (1951), the matter was finally resolved by the selection and designation of a neotype by one of us (CALLOMON 1971, 1980), a designation ratified by the International Commission on Zoological Nomenclature in 1984 (Opinion 1275).

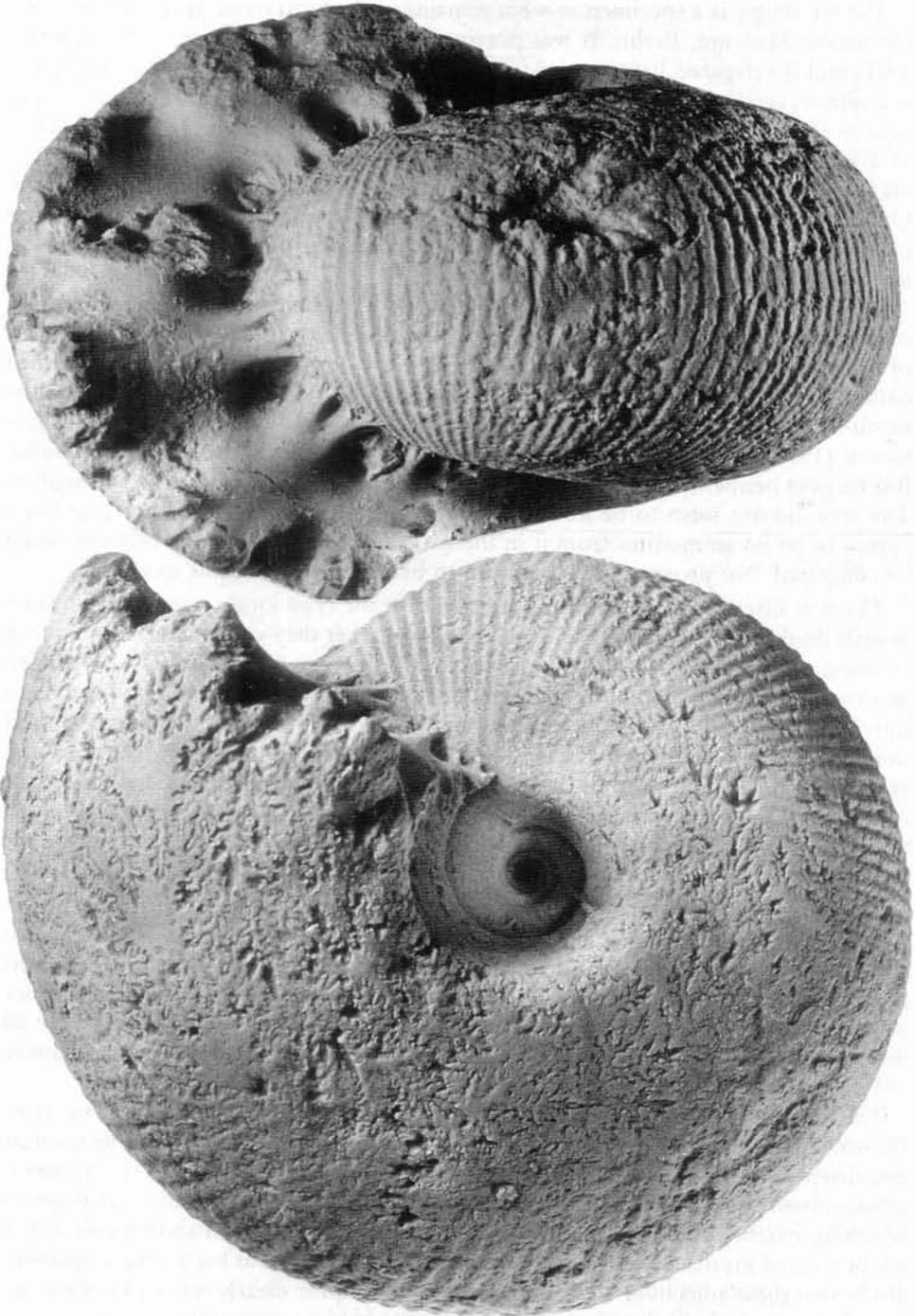


Fig. 8. Neotype of *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M]; from "dem Öttingischen" = Ipf near Bopfingen; Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone. - x1.

The neotype is a specimen in what remains of the SCHLOTHEIM collection in the Humboldt Museum, Berlin. It was previously described by one of us (CALLOMON 1971) and is refigured here as text-fig. 8. It bears one of SCHLOTHEIM's labels, and was almost certainly already in his collection in 1820. It may well have been a syntype in 1813, in which case BLAKE's type-designation of 1905 reduced it to the status of a secondary type, that of paralectotype. It was registered as "A26" in QUENSTEDT's catalogue. Apart from a brief reference to its place of origin as from "dem Öttingischen", both type locality and type horizon were unknown. The preservation is in an ironshot oolitic light brownish marl characteristic of weathered Macrocephalen-Oolith at many places.

Type locality. The reference to "dem Öttingischen" provides an important clue. It refers to the lands of the Dukes of Öttingen, a small town 15 km north-east of Nördlingen (fig. 9). In trying to locate the place of origin more closely it seemed natural to look first to the nearest outcrop of beds of the right age, which are to the north-east in Bavaria (CALLOMON 1971, p. 122). They had been mapped by GERSTLAUER (1940), who duly reported Macrocephalen-Oolith with *M. macrocephalus*. But he gave neither detailed sections nor identifiable descriptions of the ammonites. The area did not seem to be known for its fossils more generally either, and there appear to be no ammonites from it in the collections with which the neotype could be compared. No progress was therefore to be expected from this direction.

The new discoveries around the Ipf now leave the type locality and type horizon in little doubt. The only question remaining is whether they can satisfy the condition of having belonged to "dem Öttingischen". The history of the Dukes of Öttingen and their domains is complex, with amongst others the customary family schisms into Protestant and Catholic branches. But a map of 1790 shows the extent of their domains at about the time of SCHLOTHEIM. It is indicated in Fig. 9. The localities around the Ipf fall fully within these domains and were already celebrated sources of fossils from the earliest days. The preservation of the neotype agrees exactly with that of the new collections. It seems entirely to be expected, therefore, that the Ipf should have been the source of the specimen sent to SCHLOTHEIM.

#### History of classification and nomenclature

The early period. — The publication of SCHLOTHEIM's name *Amm. macrocephalus* (1813, 1820) was accompanied almost simultaneously by those of *Nautilus tumidus* REINECKE (1818) and of *Amm. herveyi* SOWERBY (1818). The close affinity of these forms was soon recognized. Identifiable figures were published under all three names by ZIETEN (1830–31), and the three species were included in the family "Macrocephali" by v. BUCH (1832, p. 146).

The first comparative systematic discussion was given by QUENSTEDT (1846: 183). He now had a large and varied collection to hand and found himself unable to draw any sharp dividing lines between species. He therefore recombined them into a single species *Amm. macrocephalus* but singled out three principal morphological types to which he attached separate additional names: *tumidus*, *compressus* and *rotundus*. The whole tone of his discussion, here and consistently throughout his writings, leave no doubt that these adjectives were intended to signify quite clearly what would to-day be called morphological variants within a variable biospecies. His discussion elsewhere of the distinction between species and variety (1857: 17) could hardly be more explicit, even by modern standards. It was unfortunate that he chose to designate these varietal distinctions in the form of Linnéan trinomina having the appearance of

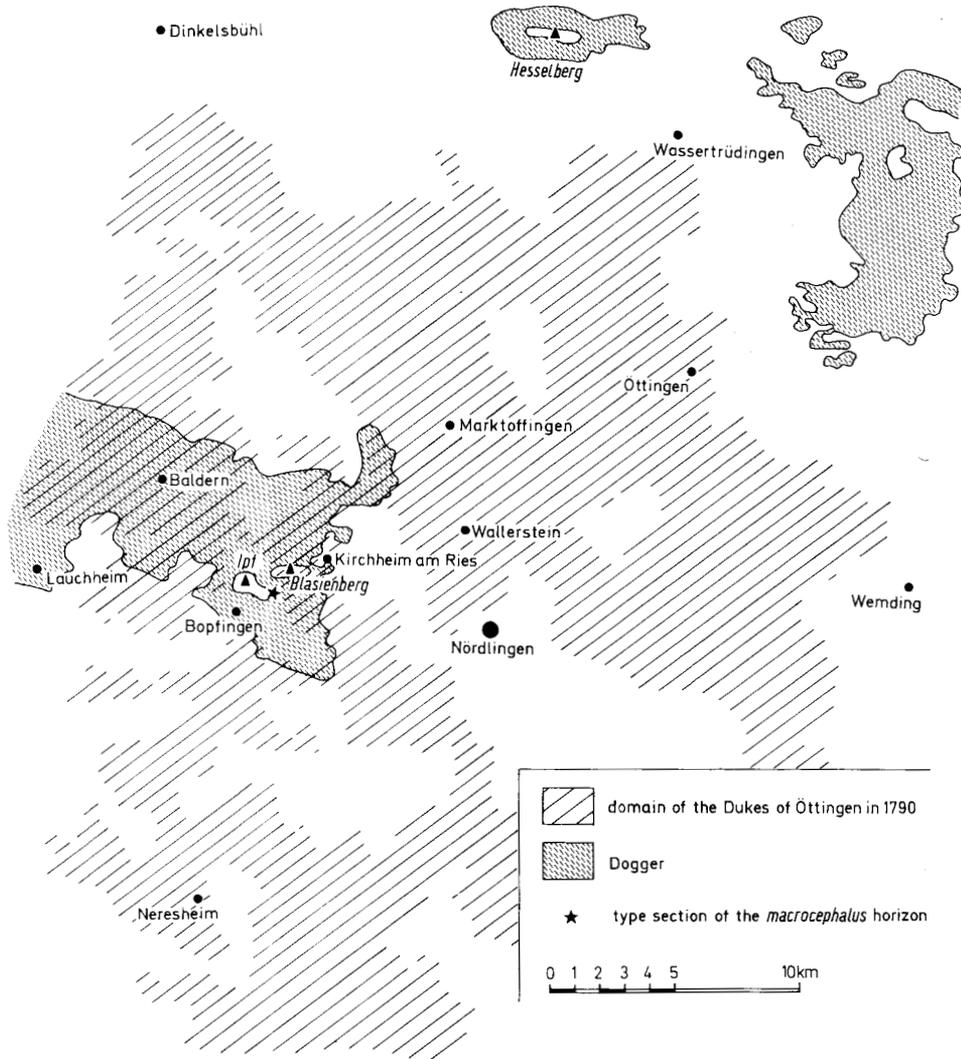


Fig. 9. The Dogger outcrop of the Ries area in comparison with the domains of the Dukes of Öttingen in 1790. Only the localities around the Ipf are falling fully within these domains.

specific and subspecific names. The nomenclatural problems of homonymy and synonymy in the classification of the ammonites created by QUENSTEDT's trinomina remain with us to this day. However, leaving aside these technical problems, QUENSTEDT's view of *Amm. macrocephalus* was that of a single, comprehensive but highly variable species.

D'ORBIGNY's view (1846: 430) was almost identical: "Coquille comprimée ou très-renflée dans son ensemble . . .". He chose to illustrate one of the compressed forms (pl. 151) and referred to it explicitly as "variété comprimée". This choice was to have long-ranging consequences. The illustrations in the *Paléontologie Française* exercised a strong and widespread influence on the interpretation of many of the classical

species of ammonites during the half-century that followed. Their high artistic quality, combining a degree of idealization with an immediately recognizable accuracy, gave them an authority that generated a comforting feeling of finality in the identification of species. D'ORBIGNY's text was less often referred to. There began in the popular conception of *Amm. macrocephalus* a drift away from the inflated, macrocephalic forms on which the species was originally founded, towards the more compressed forms as illustrated by D'ORBIGNY.

The middle period. — As new collections came in from all over the world it became increasingly necessary to refine ammonite taxonomy. The number of new species grew almost exponentially, and the continued use of the single genus *Ammonites* became quite meaningless. When ZITTEL founded the genus *Macrocephalites* in 1884 he claimed that it contained some 40 species. A list of nominal species of *Macrocephalites* compiled by LEMOINE (1910–11) contained over 70. Yet the interpretation of *M. macrocephalus* itself remained very uncertain, so much so that the name received very little use other than in a very general sense. ZITTEL gave a new figure (1884, p. 470, fig. 655) labelled "*Macrocephalites macrocephalus* SCHLOTH. sp., Callovian, Ehningen (Württemberg)" without further description and, more seriously, without indication of magnification. It showed a specimen of the same compressed morphology as that illustrated by D'ORBIGNY. There seems even to have been a widespread view that ZITTEL's figure was merely a redrawn copy of D'ORBIGNY's (see for instance BUCKMAN 1929, p. 4), despite the reference to Ehningen in the legend. In HYATT's English edition of ZITTEL ("*EASTMAN-ZITTEL*", 1900), ZITTEL's figure of 1884 was in fact replaced by a reproduction of D'ORBIGNY's. The shift in the interpretation of *M. macrocephalus* towards these compressed forms was therefore well established at the end of the last century.

The modern period. — The first firmly to point out the difference between *Amm. macrocephalus* SCHLOTHEIM and *Amm. macrocephalus* D'ORBIGNY/*Macrocephalites macrocephalus* ZITTEL was BLAKE (1905: 38). Echoing his remark (p. 50) apropos *Amm. subbakeriae* D'ORBIGNY, that "this species affords a striking example of the evil of not selecting a definite specimen as type", he formally designated BAIER's inflated specimen to be type of *Amm. macrocephalus* SCHLOTHEIM (p. 43). This left "the figure given by d'Orbigny . . . and Zittel . . . without an appropriate name". To accommodate together with others these more compressed forms he founded a new species *Macrocephalites typicus* (sic), choosing as type, however, neither D'ORBIGNY's nor ZITTEL's specimen but one from the English Cornbrash of Yorkshire. Although thus resolving the problem in theory, it remained in practice: BAIER's type specimen of *Amm. macrocephalus* SCHLOTHEIM was lost; and the assignment of *Amm. macrocephalus* D'ORBIGNY and *Macrocephalites macrocephalus* ZITTEL to *Macrocephalites typicus* BLAKE was at best subjective and open to dissent.

The next attempt to resolve the problem was by BUCKMAN (1929, written in 1922) in a remote publication that was widely overlooked. He saw the need to distinguish two things: the type of *Amm. macrocephalus* SCHLOTHEIM, and the type of *Macrocephalites* ZITTEL. For the former, he followed BLAKE and accepted the specimen figured by BAIER. He also followed BLAKE in clearly recognizing the differences between SCHLOTHEIM's species and that illustrated by D'ORBIGNY and ZITTEL. But in trying to settle the type of the genus *Macrocephalites* he made a serious error of method, one that was common at the time and one that the modern International Code of Zoological Nomenclature (1961, 1964, 1985) seeks expressly to eliminate in

Articles 61, 67 and 72. He took the type of a genus to be a specimen — the “genotype” or “genoelectotype” —, not a species: “. . . the author of a new generic name should state, when he creates it, not only which species, but exactly and without ambiguity which specimen of that species is to be taken as genoelectotype” (p. 2). The implication is that the “genotype” need not necessarily be the type-specimen of the type species. Hence “The genotype of *Macrocephalites* is *Macrocephalites macrocephalus* Zittel (not *Ammonites macrocephalus* Schlotheim) from ‘Callovian, Ehningen (Württemberg)’ (Fig. 655, p. 470)”. Later (p. 8), in discussing BAIER’s specimen of *Amm. macrocephalus*, he goes even further and states, “This form would not at the present day be regarded . . . even as the same genus as the *Macrocephalites macrocephalus* Zittel, which is the genotype of *Macrocephalites*” (a view evidently receiving support as late as 1978, by THIERRY). The situation as he saw it was therefore as follows:

Genus I: *Macrocephalites* ZITTEL, 1884

Species A: unnamed, type species, *M. macrocephalus* ZITTEL, non SCHLOTHEIM  
Specimen 1: ZITTEL, fig. 655, genotype of *Macrocephalites*

Genus II: unnamed, non *Macrocephalites* ZITTEL, 1884

Species B: type species *Amm. macrocephalus* SCHLOTHEIM

Specimen 2: BAIER, type of *Amm. macrocephalus* and genotype of genus II.

He therefore set out to ratify this scheme by publishing the unnamed taxa in his Type Ammonites:

Species A: *Macrocephalites verus* nov., BUCKMAN 1922 (T.A. 4, pl. 334A, B).

Genus II: *Macrocephalicerias* nov., BUCKMAN, 1922 (T.A. 4, pl. 313); type species *Macrocephalicerias macrocephalum* (SCHLOTHEIM).

He went further and tried to reillustrate ZITTEL’s “genotype” by borrowing the specimen, if it existed, from Munich (1929, p. 5). The result was to add even further to the confusion. We now know that DACQUÉ sent him the wrong specimen. The holotype of species A, *M. verus*, figured by BUCKMAN on his pl. 334, was not ZITTEL’s specimen and hence not the “genotype” of *Macrocephalites*.

To sort out this confusion in preparation for the ammonite volume of the Treatise ARKELL (1951) decided the only practical course would be to apply to the International Commission to use its plenary powers to impose a compromise solution in which (i) *Amm. macrocephalus* SCHLOTHEIM was to become the type species of *Macrocephalites* (overlooking that this had already been done by LEMOINE); (ii) that the specimen figured by BUCKMAN was to become the type of *Amm. macrocephalus*. Being already holotype of *M. verus*, this would make that species permanently a junior objective synonym of *M. macrocephalus*. The shift in interpretation from SCHLOTHEIM’s inflated forms to D’ORBIGNY’s and ZITTEL’s compressed forms would have been complete. Anticipating a successful outcome, ARKELL reproduced BUCKMAN’s figures of *M. verus* both in the Treatise (1957, p. L. 294, fig. 351) and in the Jurassic Geology of the World (1956, pl. 37, fig. 6) as *M. macrocephalus*, in this latter work in its role as index-species of the Macrocephalus Zone.

ARKELL’s proposals were however never acted upon, as clearly stated in 1971 (CALLOMON, p. 115). Despite this, the belief that they had continued to persist (MAUBEUGE 1975, p. 126; THIERRY 1978, p. 205). There were a number of reasons for the Commission’s failure to act, but the strongest reason was the discovery that the specimen figured by BUCKMAN had been lost during the war. This was already admitted by ARKELL in 1956 (pl. 37, legend to fig. 6). Had the Commission ratified his proposals, it still would not have solved the problem: there still would not have

been an actual specimen. Neither would it have confirmed the additional value of the type specimen that ARKELL had stressed in his application, that of becoming zonal index of the *Macrocephalus* Zone, because neither the locality nor horizon were known any more precisely than those of almost any other specimen in the old collections labelled "*M. macrocephalus*". The discovery that the holotype of *M. verus* was not even the specimen figured by ZITTEL was to come later, but it would have compounded the confusion even further.

The final steps were taken by one of us (CALLOMON) in 1971. They rested on a solution,

(i) that was fully in accord with the International Code as then and now in force and that required no action by the Commission under its plenary powers;

(ii) that restored the interpretation of *Amm. macrocephalus* to something close to its original sense as understood by SCHLOTHEIM, ZIETEN, QUENSTEDT and D'ORBIGNY;

(iii) that left *Macrocephalites verus* BUCKMAN, 1922, as an independently available name to be applied to ZITTEL's species, thereby expressing the perfectly valid taxonomic distinctions between SCHLOTHEIM's and ZITTEL's species;

(iv) that retained both SCHLOTHEIM's and ZITTEL's species in the genus *Macrocephalites*.

The outcome was the neotype as described at the beginning of this account. The only outstanding uncertainty lay in the precise age of the species as exemplified by the neotype, and hence of its relation to the existing nomenclature of the standard chronostratigraphy.

Specific taxonomy. — The minimum typological definition of a species is provided by its type specimen. In conventional classification, the species is then amplified by including such other specimens as the classifier considers to be "related". The criteria of relationship in fossils can rarely rise above the level of morphological similarity expressed in terms of distinguishable "characters". The fluid state of classification revealed by the literature of almost any species, including *M. macrocephalus* par excellence as outlined above, reflects merely varying degrees of importance attached by taxonomists to different characters. Such "conventional" species are therefore morphospecies, and as morphologically similar specimens are often found over a range of strata, morphospecies in general have vertical, stratigraphical extensions. A classification into morphologically distinguishable, parallel morphospecies having time-ranges is therefore a vertical classification. It is purely descriptive and largely subjective.

Of more fundamental interest is the biospecies in a zoological sense. A biospecies consists of individuals that are related genetically. These relations are expressed in the ability of the members of the species to interbreed. Morphological relationships take secondary place and may not always be immediately obvious. The recent history of dimorphism in ammonites provides a striking example. The importance of biospecies in palaeontology lies in the fact that it is they that are the units that evolve in time; and it is the mapping of patterns of evolution, of phyletic lineages, of phylogeny, to which palaeontology makes a unique contribution and in which lies its greatest interest.

From the definition it follows that a biospecies has, strictly speaking, a time-range of at most a few generations, and that past biospecies can never be identified in fossil assemblages. Fortunately, the gene-pool of most biospecies evolves locally very

slowly in comparison with the turn-over rate of successive generations, so that an assemblage of remains of organisms that lived over an extended sampling-interval may approximate quite closely to the remains of a biospecies. The common experience of collecting shells on the seashore confirms this. The important question in palaeontology is, therefore: can a biostratigraphical sampling interval be made sufficiently narrow for its fossil assemblages to give an adequate, average representation of fossil biospecies? In ammonites, the answer is yes. If two successive fossil assemblages are indistinguishable, no significant evolution has occurred, and that part of the genome determining the structures preserved as fossils has remained unchanged. Examples of successive indistinguishable ammonite assemblages are well known. A bed containing such an effectively isochronous assemblage, distinguishable from other such assemblages, has come to be referred to simply as a faunal horizon. The actual time-interval represented by a faunal horizon is generally not precisely determinable, but can range in ammonites from as little as one day to as much as 100 000 years (for a more extensive discussion, see CALLOMON 1985b). An evolving lineage is therefore seen in the fossil record as a succession of what are regarded as effectively isochronous fossil biospecies, or transients. A classification that incorporates this additional, infra-morphological dimension of time is a phylogenetic classification. Because the units are the horizontal slices in a vertical tree, the classification at the level of the species is sometimes referred to as a horizontal classification. We note that the type specimen of a nominal species now automatically acquires also a second objective function. It defines the type horizon of the species, or, in cases in which the same Linnéan specific name is used for a succession of transients (cf. CALLOMON 1985b, p. 57), that of the type transient of the species.

The problem of the vertical dimension of time having been resolved, there remains the question of the actual identification of a biospecies and its extent within an isochronous fossil assemblage. How many species were there, living side by side? The only guide can now be morphological, and the problem is to recognize correctly the range of intraspecific variability of a species. The hope is that the presence of more than one taxon would be revealed by a bi- or polymodal distribution-function of one or more quantifiable characters. Sometimes this works very well. The bimodal distribution, for example, of the maximum adult size of an isochronous assemblage of otherwise similar ammonites continues often to be one of the most obvious signs of dimorphism, *Macrocephalites* included. But to demonstrate bimodality statistically beyond reasonable doubt (e. g. within confidence-limits of 95 %) can make heavy demands on material. The number of well-preserved specimens available has to be considerable. In ammonites this is only quite rarely the case. Most commonly, a small collection gives an initial impression of being made up of several species (morphospecies). To demonstrate the contrary, that the apparent polymodality is statistically insignificant and arises merely from random fluctuations in an inadequate sample, is equally demanding. Being an evaluation of negative evidence, it is less commonly attempted. The first indications tend to come from the effects of additional material, when new specimens fall between, rather than into, the previously adopted "species". But even when an assemblage may reasonably be regarded as probably unimodal in morphology, its identification with a single species must remain a presumption. In ammonites and bivalves, there are reasons to believe that such presumptions are justified. In gastropoda, they would be highly hazardous.

In the present example of *Macrocephalites macrocephalus*, we adopt a horizontal,

biospecific classification. The stratigraphical controls, combined with the homogeneity in the non-quantifiable details of sculpture and ribbing readily apparent to the eye and shared by all the shells, leave us satisfied that the assemblage from bed 5 may be treated as effectively isochronous. The number of specimens is sufficient to apply statistical tests to distribution-functions of variability in some characters. We conclude that the assemblage is monospecific, albeit dimorphic as in other species of the genus. We have discussed the underlying principles at some length, for in this respect, that of specific diversity, our conclusions differ radically from those of THIERRY (1978), who claimed to be following the same principles. These differences are discussed further below.

#### Material:

##### Macroconchs:

- (a) from the new excavation: ca. 50, including fragmentary specimens, from bed 5 in situ or unequivocally by matrix, and 1 from the boundary between the top of bed 5 and the base of bed 4;
- (b) collection SCHWARZ: 30, from "Blasienberg", ca. 500 m east of the new excavations (see Fig. 9); bed 5 by matrix. (DANIEL SCHWARZ lived in Bopfingen-Oberdorf and was a keen local collector).
- (c) the neotype: Humboldt Museum, Berlin, QUENSTEDT catalogue A26.

Total: 80+; of these, 23 have some of the adult bodychamber preserved and 52 are sufficiently well-preserved to give reliable measurements.

Microconchs: 1 complete adult and some fragments.

#### Description

Macroconchs. — Dimensions of the shell are summarized in Table 1. The only character calling for special comment is the whorl-breadth  $B$ , which measures the degree of inflation. Its variability and development during growth have therefore been analysed statistically. As usual, it is expressed in reduced form  $b$ , as percentage of the shell-diameter,  $D$ :

$$b = (B/D) \times 100 (\%)$$

Conventionally, the co-ordinate taken to measure the growth of the shell is also the diameter, but for comparative purposes in organisms developing by linear allometric growth, an exponential growth-function is more appropriate. In normally coiled ammonites, as is well known, the radius-vector and hence diameter of the shell in the plane of the spiral follows the simple exponential relation

$$r_{\theta} = r_0 \cdot e^{a\theta} \quad (1)$$

where  $\theta$  is the spiral angle in radians measured from an arbitrary origin at which  $r_{\theta} = r_0$ , and  $a$  is a constant. It is useful to change scale, to measure the spiral angle in terms of whorls, and for ammonites the most convenient unit is the half-whorl ( $\theta = n = 180^\circ$ ). Then

$$r_n = r_0 \cdot \rho_n^n \quad (2)$$

where  $\rho_n$  is the spiral half-whorl constant, and  $n$  is the number of half-whorls measured from some angle at which the radius-vector has the value  $r_0$ . Then a similar relation holds for the shell diameter,  $D$ :

$$D_n = D_0 \cdot \rho_n^n \quad (3)$$

The usefulness lies in the fact that

$$\rho_n = r_{(n+n)}/r_n = D_{(n+n)}/D_n$$

It is the ratio of the diameters of the shell at half-whorl intervals. Conversely, measuring the diameters at half-whorl intervals is a simple way of determining the spiral

constant. For other intervals, e.g.  $\theta = 2n = 360^\circ$  or  $\theta = n/2 = 90^\circ$ ,

$$\rho_{2n} = \rho_n^2; \quad \rho_{n/2} = \sqrt{\rho_n}$$

(The relationship between the constant  $a$  in equation (1) and  $\rho_n$  is given by  $\ln \rho_n = a_n$ . To locate the "centre" of the ammonite,  $r_n = D_n \cdot [\rho_n / (\rho_n + 1)]$ . An alternative parameter sometimes used to define a logarithmic spiral is the tangential angle,  $\alpha$ . Then  $\tan \alpha = 1/a = n / \ln \rho_n$ .)

In the present case, 23 specimens of *M. macrocephalus* from bed 5 retained complete, adult phragmocones. The mean adult diameter  $\langle D_\Phi \rangle$  of the phragmocone comes to  $158 \pm 9$  mm, where the uncertainty is twice the standard error,  $2\varepsilon(\langle D_\Phi \rangle)$ . The standard deviation  $\sigma(D_\Phi)$  expresses the distribution of the individual values of the diameter about its mean. This mean adult phragmocone diameter has here been chosen for the value of  $D_0$  in the spiral formula of equ.(3). The spiral constant  $\rho_n$  was found to be 1.38;  $\alpha = 84.15^\circ$ .

The development of the whorl-breadth during growth is shown in Figure 10–12. Average values of  $b$ ,  $\langle b \rangle = \langle B/D \rangle$ , have been calculated for five successive half-whorl intervals. Their uncertainties ( $\pm 2\varepsilon$ ) are indicated by the hatched fields, and their spreads are indicated by the horizontal bars at  $\pm 2\sigma(b)$ . We see that with the exception perhaps of a small increase on the adult bodychamber, the mean whorl-breadth  $\langle b \rangle$  does not change significantly over the last two whorls of the phragmocone, from its overall mean value of 68% of the whorl-diameter, even when that diameter increases four-fold.

We may therefore combine without serious error the measurements of whorl-breadth over a range of shell-diameters to test their distribution about the mean. The results are shown in Figure 12. The measurements are grouped into class-intervals of 5% in  $b$  along the abscissa. Three histograms of distribution are shown:

- (a) dense shading: shell-diameters less than 125 mm;
- (b) light shading (counted down to the abscissa): shell-diameters greater than 125 mm;
- (c) unshaded: all measurements ( $N=57$ ).

Superimposed is a Gaussian curve with the same normal distribution parameters as those of all the measurements. The indications of Figure 12 are clear. The distribution does not depart significantly from unimodal, although it may be somewhat skewed in the direction of the less inflated variants; and the variability is considerable, with a standard deviation of 12% about the mean. These conclusions are discussed further below. The difference between the compressed and inflated extreme variants may be judged visually in the specimens illustrated in Pl. 3, fig. 1, and Pl. 3, fig. 2.

Among the other morphological characters, the cross-sections are subcircular to depressed at all stages of growth, with well-rounded umbilical margins. The ribbing is dense and fine, with little differentiation between primaries and secondaries, and fades gradually towards the end of the phragmocone. The bodychambers are smooth and revert to being compressed, with strong uncoiling of the umbilical seam, as typical of the genus as a whole. Septal sutures are also typical.

Microconch. — The one good specimen is shown in Pl. 5, fig. 1. It is nearly complete, with about half a whorl of bodychamber. The slight uncoiling of the umbilical seam and modification of the ribbing on the last quarter whorl indicate that it is adult. Its ontogeny is included schematically in Fig. 11, which shows that the

Tab. 1. Dimensions of the shell of *Macrocephalites macrocephalus* (SCHLOTH.) from bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigii Zone; Ipf near Bopfingen.

	Range	Mean value $\langle \rangle \pm 2\epsilon \langle \rangle$	Standard deviation $\sigma/\text{mm}, (\sigma/D, \%)$	N
<b>Macroconchs</b>				
<u>Diameter of adult phragmocone</u>				
$D_\phi$ , - mm	135 - 220	$158 \pm 8.7$	21 (13%)	23
--- cf. neotype, - mm	---	145	---	1
<u>Adult bodychamber, length</u>				
- whorls	-	0.75	-	2
<u>Whorl-height, coefficient</u>				
$h = H/D$ , $D = 116-160$ mm, %	46 - 51	$49.6 \pm 0.7$	1.5 (3%)	20
61-115 mm, %	45 - 51	$48.9 \pm 0.9$	1.7 (3%)	16
32- 60 mm, %	40 - 50	$46.6 \pm 1.7$	2.8 (6%)	11
--- neotype, 110-140 mm, %	---	51	---	1
<u>Whorl-breadth, coefficient</u>				
$b = B/D$ ,				
$n = 0 - 1$ , $D = 160-221$ mm, %	59 - 91	$75.6 \pm 6.8$	10.2 (13%)	9
-1 - 0 116-159 mm, %	57 - 83	$68.1 \pm 4.0$	7.9 (12%)	16
-2 - -1 84-115 mm, %	59 - 71	$65.2 \pm 3.0$	4.2 (6%)	8
-3 - -2 61- 83 mm, %	54 - 79	$65.0 \pm 3.3$	6.1 (9%)	14
-4 - -3 44- 60 mm, %	55 - 80	$68.1 \pm 5.6$	8.3 (12%)	9
-5 - -4 32- 43 mm, %		74		1
- all - %	54 - 91	$68.2 \pm 2.2$	8.0 (12%)	57
- neotype, 110-140 mm, %	---	67-68	---	1
<u>Umbilical width, coefficient</u>				
$u = U/D$ , $D = 116-160$ mm, %	13 - 19	$15.5 \pm 0.7$	1.5 (10%)	19
61-115 mm, %	12 - 21	$15.4 \pm 1.2$	2.3 (15%)	16
32- 60 mm, %	16 - 23	$18.4 \pm 1.6$	2.5 (14%)	11
- neotype, 110-140 mm, %	---	16	---	1
<b>Microconch</b>				
$D_\phi$ , - mm	---	58	---	1
$h = H/D$ , $D = 65$ mm, - %	---	49	---	1
$b = B/D$ , $D = 65$ mm, - %	---	53	---	1
$u = U/H$ , $D = 65$ mm, - %	---	17	---	1

phragmocone of the macroconch is about three half-whorls longer than that of the microconch. The coiling, cross-section and style of ribbing on the inner whorls, as far as these are visible, are very similar to those of the macroconchs at comparable diameters up to 60 mm.

Treated as a morphospecies in isolation, this microconch would be classified as a typical *M. (Pleurocephalites) sp.*

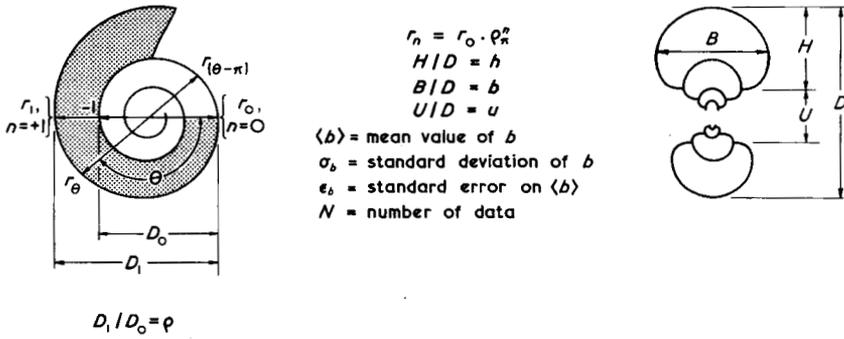


Fig. 10. Measurements and proportions.

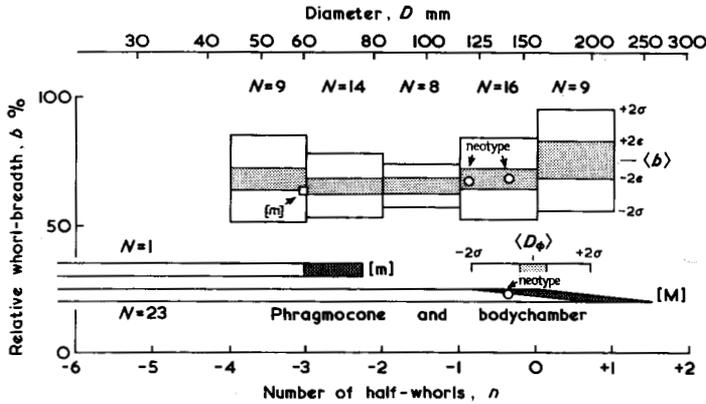


Fig. 11. The ontogenetic development and variability of the relative whorl-breadth  $b$  and its variability as a fraction of whorl-diameter  $D$  in *Macrocephalites macrocephalus*. Spiral half-whorl constant  $\rho = 1.38$ ; mean maximum diameter of adult macroconch phragmocone  $D_0$  (max) =  $D_0 = 160$  mm.

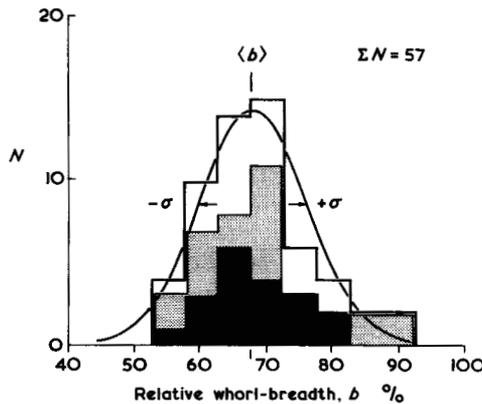


Fig. 12. The variability of the whorl-breadth  $b$  as a fraction of whorl-diameter  $D$  in *Macrocephalites macrocephalus* expressed as histograms of distribution about the mean. Solid: at shell-diameters below 125 mm; hatched: at shell-diameters greater than 125 mm; top, unhatched: all. Equivalent Gaussian curve superposed.

Comparisons and distribution. — Among macroconchs, the slightly earlier *M. megalocephalus* is similar in range of inflation to *M. macrocephalus* although the more compressed variants with subtriangular whorl-section are relatively more common (cf. *Tmetocephalites septifer* BUCKMAN, 1923, pl. 433, of about this age) and the species is even bigger. The ribbing is also less densely-spaced.

Elsewhere, it is a curious fact that there are up to now no unquestionable figures or descriptions of the true *M. macrocephalus* in the literature from anywhere, despite the fact that beds of the appropriate age are almost certainly widely present. The main reason, already mentioned above, may be strong polarizations of the dimorphic ratio. At the IpF, the ratio of [M]:[m] is around 20:1, and the microconch is known from only a single well-preserved specimen. Other places from which *Macrocephalites* of the lower Koenigi Zone have been described include Poix in the Ardennes (CORROY 1932), Vendée, Deux-Sèvres and Sarthe in western France (F. DOUVILLÉ 1943), and southern England (BUCKMAN). Yet in these works the only identifiable adults are microconchs. Among these, the best known are those from England:

- M. (Pleurocephalites) lophopleurus* BUCKMAN, 1922 (Pl. 284)  
 — — *folliformis* BUCKMAN, 1922 (Pl. 348)  
 — — *liberalis* BUCKMAN, 1925 (Pl. 558)

from the Gowerianus Subzone, *metorchus* horizon of Chippenham/Wiltshire. To these should probably be added:

- M. (Pleurocephalites) jacobi* (CORROY, 1932) (Pl. 5, figs. 5, 6)  
 — — *subtumidus* WAAGEN. — CORROY (Pl. 10, figs. 1, 2)  
 — — *elephantinus* WAAGEN. — CORROY (Pl. 11, figs. 1, 2)

from Poix. Besides the specimens figured by BUCKMAN the English collections contain several dozen more, including ones that match those from Poix. Together they give a good impression of the range of variation. They differ consistently from the specimen from the IpF, which is more involute and more finely ribbed. Conversely, there are microconchs from the *megaloccephalus* horizon of the Wutach that do resemble the *lophopleurus* assemblage closely, even if they are not identical. Another similar but also not identical assemblage in the collections of the University of Poitiers, so far undescribed, occurs at Pamproux (Deux-Sèvres), in bed 1 of CARIOU (1980, p. 3, Fig. 2); but this lies below the horizon of *Kheraicerias prahequense* and is thus somewhat older even than the *megaloccephalus* horizon. But two specimens in Poitiers, one [M] and one [m], that resemble *M. macrocephalus* very closely indeed came from St. Vincent-sur-Jard (Vendée), beds 4b–5 of CARIOU (1980, fig. 22), near the top of the *prahequense* horizon and immediately below the first levels with *Reineckeia* and *Proplanulites* there.

Discussion. — The most recent comprehensive systematic treatment of *Macrocephalites* is that by THIERRY (1978). Comparisons with this work fall into two categories: nomenclatural and taxonomic.

The principal nomenclatural difference has already been discussed. THIERRY's decision to shift the interpretation of *M. macrocephalus* to ZITTEL's concept of the species, now called *M. verus* BUCKMAN, means that *Amm. macrocephalus* as interpreted here and already defined in 1971, does not appear in his genus *Macrocephalites* at all. It would presumably have been included in his genus *Kamptokephalites* (see below). But even leaving aside this nomenclatural point, for those wishing to retain separate morpho-subgeneric divisions within *Macrocephalites*, what should *M. verus* now be called? The only appropriate and available name appears to be *Tmetocephalites* BUCKMAN (see the list of generic names given above). The holotype of the type

species, *T. bathytmetus* (1923, pl. 373), almost certainly came from Württemberg, as BUCKMAN correctly surmised. It is septate to only about 60 mm and carries a little bodychamber, but the absence of any of the usual signs of maturity and the complexity of the septal suture leaves no doubt that it is a macroconch, probably juvenile. In all other respects it resembles *M. verus* so closely that it may safely be regarded as a junior synonym. *M. (T.) verus/bathytmetus* occurs in the lowest part of the Lower Callovian, lower Herveyi Zone, Keppleri Subzone, *keppleri-suevicum* horizons. It is perhaps commonest in the *quenstedti* horizon. Occasional specimens may occur as extreme variants already in the *hollandi* horizon of the Upper Bathonian. This relatively early age of *M. verus* was also already known in 1971, but THIERRY (p. 440) shows it as ranging from the Kamptus Subzone through what is now the lower half of the Koenigi Zone. (Even more remarkable, he puts the ancestor of *M. verus*, *M. jacquoti* = *Amm. macrocephalus compressus* QU., into the Calloviense Subzone above. Its proper level is Discus Zone and *keppleri* horizon, persisting into the *quenstedti* horizon.)

#### 4.2. Family Reineckeidae HYATT, 1990

##### Subfamily Reineckeinae HYATT

##### Genus *Reineckeia* BAYLE, 1878

Type species: *Nautilus anceps* REINECKE, 1818.

REINECKE's work has become more accessible through a translation by HEUBER and HELLER in ZEISS (1972). The text suggests that the specimen figured by REINECKE was the only one he had, hence holotype. It has long been lost. It consisted of a small, coronate, flat-ventered cadicone pyritized nucleus, recognizable as a *Reineckeia* but little more. The modern interpretation of this venerable species, type species of one of the most important groups in the Callovian and index species of another of OPPEL's original Zones, has therefore been almost as uncertain as that of *Amm. macrocephalus*. As there, a major source of the uncertainty lay in its unknown age. REINECKE's allusions to its preservation and origin near Ützing, in northern Franconia, suggested the famous "Goldschnecken" fauna from that locality whose age is latest Lower Callovian, Enodatum Subzone. But a revision of the Franconian ammonites, including those from Ützing, by KUHN (1939) contains nothing resembling REINECKE's figure. Instead, several specimens very close to the latter, figured by SPATH (1928, p. 255, p. 44, figs. 6a-c) and JEANNET (1951, p. 125, pl. 48, figs. 2, 3) all come from Neidlingen, south of Göppingen in the central Swabian Alb, not far from the classical localities of Boll and Gammelshausen, from which the species had already been cited by OPPEL (1857, p. 519), and nowhere near Ützing or northern Franconia as stated. These were collected by MODEL in the 1920's (MODEL 1935, p. 339) who sold material both to ROLLIER in Zürich and to the British Museum in London. Recent excavations for a motorway at nearby Gruibingen have yielded new collections bed by bed. The Enodatum, Medea and Jason Subzones could be clearly distinguished. Pyritized nuclei exactly like those collected by MODEL and closely resembling REINECKE's figure came from the lower Jason Subzone. The Medea Subzone yielded no identifiable *Reineckeia*. The Enodatum Subzone is relatively rich in *Reineckeia*, but the forms are quite different. The age of *R. anceps* seems therefore to be definitely Jason Zone, upper part, confirming the conclusions based on French material arrived at by CARIOU (1984, p. 220); and there seem to be no obstacles in following his widening of the interpretation through all growth-stages up to the

complete adult macroconch as illustrated in his pls. 33–34, all from the Medea Subzone. As for Ützing, the Jason Zone does occur in the region (REUTER 1908, p. 26) even if not at Ützing itself, and well above the "Goldschnecken". REINECKE's reference could therefore have been correct.

*Reineckeia quenstedti* nom. nov.

pro *Reineckeia franconica* (QUENSTEDT, 1886, non SCHLOTHEIM, 1813)

Pl. 6, figs. 1a, b; text-fig. 13

- non 1813 *Ammonites franconicus* SCHLOTHEIM, p. 101.  
 non 1847 *Ammonites anceps* REINECKE. — D'ORBIGNY, p. 462 partim, pl. 167, figs. 1–3 only. — [Syntype III: = *Reineckeia substeinmanni* LEMOINE, 1910, holotype; refigured by BOURQUIN 1967, pl. 27, figs. 1a, b]  
 non 1878 *Reineckeia anceps* REINECKE, sp. — BAYLE, p. 56, fig. 1. — [Syntype IV; refigured by BOURQUIN, pl. 27, fig. 3]  
 1886 *Ammonites anceps franconicus* QUENSTEDT, p. 633, pl. 74, fig. 39, 39r [Syntype I = designated lectotype]; fig. 39q, 39 l [Syntype II].  
 1928 *R. franconica* QUENSTEDT. — SPATH, p. 259.  
 1955 *R. (Reineckeia) franconica* (QUENSTEDT). — ZEISS, p. 248.  
 1984 *Reineckeia (Tyrannites) franconica* (QUENSTEDT). — CARIOU, p. 201.  
 1985 *Reineckeia (Reineckeia) franconica* (QU.). — SCHLEGELMILCH, p. 140, pl. 56, fig. 2 (lectotype designated there).

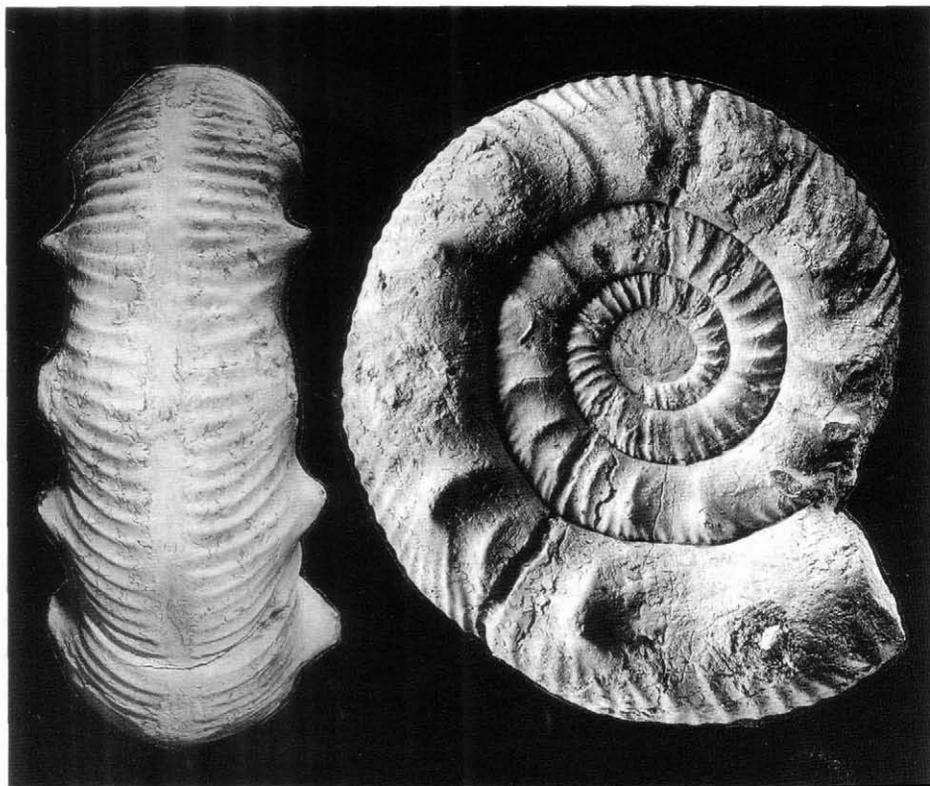


Fig. 13. Lectotype of *Reineckeia quenstedti* nom. nov. pro *R. franconica* (QUENST. non SCHLOTH.); Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; "Nipf" = Ipf near Bopfingen.

Lectotype: Syntype I, QUENSTEDT (1886, p. 74, fig. 39, 39r), designated by SCHLEGELMILCH (1985), refigured here (fig. 13).

Type locality and horizon: Ipf, bed 5; lower Koenigi Zone, *macrocephalus* horizon.

Discussion. — We do not wish to go into the systematics of the genus *Reineckeia* here beyond the implications of the new material obtained at the Ipf. They are twofold: nomenclatural, and stratigraphic.

As the synonymy indicates, the name *franconicus* attached to *Reineckeia* entered the literature as one of QUENSTEDT's unfortunate trinomina in 1886 and has enjoyed a certain popularity ever since, being retained as that of a clearly distinguished species in the most recent monographic revision by CARIOU (1984). The species was based on an indefinite type series which included at least the four figured syntypes listed in the synonymy. There was thus no holotype, despite CARIOU's reference to syntype I as such. All authors have however based their interpretations on QUENSTEDT's figures, and the designation of one of these (see fig. 13) as lectotype by SCHLEGELMILCH (1985) was only a formality. Of the other syntypes, D'ORBIGNY's III became holotype of *Reineckeia substeinmanni* LEMOINE, and this species has been subsequently reunited with *R. anceps* by CARIOU (1984, p. 220), as has BAYLE's syntype IV.

QUENSTEDT's original species has therefore been subdivided into two taxa of considerably different ages: *R. franconica* s. s. of the lower Koenigi Zone, and *R. anceps* of the lower Jason Subzone. But the name *Amm. franconicus* was already preoccupied by SCHLOTHEIM, who applied it to a species of Upper Pliensbachian *Pleuroceras* [HOWARTH 1958, p. 37, lectotype text-fig. 14, p. 38; = *Pleuroceras spinatum* (BRUGUIÈRE), subj.]. We believe that *R. franconica* (QU.) may be a junior subjective synonym of *Reineckeia rehmanni* (OPPEL, 1857; p. 551), but there are still serious systematic problems to be resolved in this species also. But in any case, before considering questions of conspecificity of two taxa, both should be validly named. We therefore propose the nomen novum *Reineckeia quenstedti* for QUENSTEDT's taxon, type series unchanged, to resolve the homonymy with SCHLOTHEIM's.

### *Reineckeia grossouvrei* PETITCLERC sensu CARIOU

Pl. 6, fig. 2

? 1915 *Reineckeia grossouvrei* PETITCLERC, p. 96, pl. 11, fig. 3 (type).

1984 *Rehmannia (Rehmannia) grossouvrei* (PETITC.). — CARIOU, p. 41; pl. 2, fig. 2; pl. 3, figs. 1a, b, 2a, b.

Material: One fragment, part of two wholly septate whorls. Ipf, bed 5, *macrocephalus* horizon (SMNS 61624/52).

Discussion. — The main purpose of describing the present imperfect specimen is to show that densely-ribbed, non-coronate forms of *Reineckeia* also occur already in the earliest faunas. The specimen differs considerably from PETITCLERC's type, but does resemble some of the forms among the analogous early fauna of horizon III, Rehmanni Subzone, of western France described by CARIOU and grouped together by him under the name *grossouvrei*.

There is also a resemblance to *R. greppini* (OPPEL), a cast in Lyon of whose type was figured by BOURQUIN (1967, p. 34, fig. 1). This came from a then unknown horizon near Trimbach in the northern Jura, which was later identified as early Middle Callovian by ROLLIER (1923, p. 382). Such an age received support from additional material closely resembling the type found in the Medea Subzone, lowest

Middle Callovian, of western France (CARIOU 1984, pl. 12, figs. 2, 3). *R. greppini* is therefore considerably younger than the form from the Ipf.

4.3. Family Perisphinctidae STEINMANN, 1890  
Subfamily Proplanulitinae BUCKMAN, 1921

Genus and subgenus *Proplanulites* TORNQUIST, 1887

*Proplanulites* (*Propl.*) cf. *subcuneiformis* and cf. *fabricatus* BUCKMAN, 1921 [m]  
Pl. 2, figs. 2, 3

cf. 1921 *Proplanulites subcuneiformis* BUCKMAN, p. 37, pl. 227 [m].

cf. 1921 *Proplanulites fabricatus* BUCKMAN, p. 36, pl. 251 [m].

Material: One fragment of bodychamber (SMNS 61624/51) and one phragmocone (KÖSTLIN coll., SMNS 28710): Ipf, bed 5, *macrocephalus* horizon; and one fragment (SMNS 62375), bed 6a, *megalcephalus* horizon.

Discussion. — The fragment shown in Pl. 2, fig. 2, is that of an adult microconch. Comparison with BUCKMAN's figure is purely morphospecific. His creation of 30 new nominal species based on English types alone (1921, p. 34–42) continues to serve as little more than a terrible example. Abundant new collections in recent years leave little doubt that the assemblage from any one faunal horizon belongs to a single variable, dimorphic biospecies; that the assemblages changed only slowly with time; that individual variants or morphs have considerable vertical ranges; that the value of *Proplanulites* as stratigraphical indicator is therefore low; and that a precise assignment of most of the existing nominal species to their correct horizons may remain impossible. Given enough material, it may be possible in the English Lower Callovian to distinguish three, perhaps four, successive assemblages of *Proplanulites*. The specimens shown here could fit into the lowest of them, in the Gowerianus Subzone, but little more can be said. This Subzone is also the source of *P. koenigi* itself (lectotype figured by ARKELL 1956, pl. 27, fig. 4), and it and *P. subcuneiformis* could represent merely the most involute and evolute microconch extremes in variability of the same species. *P. fabricatus* is the most typical, intermediate form.

Subgenus *Crassiplanulites* BUCKMAN, 1921

*Proplanulites* (*Crassiplanulites*) *basileus* BUCKMAN, 1921 [M]  
Pl. 9, fig. 2

1921 *Proplanulites basileus* BUCKMAN, p. 34, pl. 252 [M]

Material: One phragmocone, probably complete and adult, septate to 230 mm; old collection (SMNS 61952), Ipf, bed 5 by matrix.

Discussion. — These large, subdiscoidal forms that become wholly smooth on the outer whorls are common and highly characteristic of the English Gowerianus Subzone. The type of *Crassiplanulites crassicosta* BUCKMAN, 1921 (pl. 228A, B), the type species of the genus, in contrast retains strong, coarse ribbing to large diameters and typifies the later faunas of the Calloviense Zone and Subzone. Although BUCKMAN introduced the generic name (1921, p. 41) to indicate this feature of a sculptural character, it is now the only such name based on a macroconch morphospecies and, as such, may continue to fulfil some useful purpose at subgeneric level.

4.4. Family Cardioceratidae SIEMIRADZKI, 1891  
 Subfamily Arctocephalitinae MELEDINA, 1968

Genus *Chamoussetia* DOUVILLÉ, 1911

*Chamoussetia* cf. or aff. *phillipsi* CALL. & WRIGHT, 1989

- v 1856 *Ammonites Chamousseti* D'ORBIGNY. — QUENSTEDT, p. 535, pl. 70, fig. 21.  
 v 1887 *Ammonites Chamousseti* D'ORBIGNY. — QUENSTEDT, p. 806, pl. 90, figs. 18, 18p.  
 v cf. 1989 *Chamoussetia phillipsi* CALLOMON & WRIGHT, 1989 (nom. nov. pro *Amm. lenticularis* PHILLIPS, 1829, non YOUNG & BIRD, 1828), p. 803, pl. 89, figs. 2a–c.

Material: One incomplete, fragmentary phragmocone; Ipf, bed 5, *macrocephalus* horizon (SMNS 61624/14) and the specimen of QUENSTEDT (1856; 1887) from the same locality and the same bed by matrix.

Discussion. — A recent revision of English material revealed that PHILLIPS' traditional name for a well-known Yorkshire species of the middle Koenigi Zone was preoccupied; and that another well-known species from southern England described by BUCKMAN under PHILLIPS' name (*Ch. buckmani* CALL. & WRIGHT, 1989, type *Ch. lenticularis* BUCKMAN, non PHILLIPS, 1924, pl. 462, refigured CALLOMON & WRIGHT, pl. 90) is slightly older, lower Koenigi Zone. The holotype of *Ch. chamousseti* (D'ORBIGNY) (1847, pl. 155, also refigured by CALLOMON & WRIGHT, text-fig. 3, p. 808) is different again, nothing exactly like it having been found in England. It came from an unknown level at Mont-du-Chat, Chanaz, Savoie, and remains so far unique.

The new specimen from the Ipf resembles *Ch. phillipsi* in inflation and whorl-section, but its inner whorls are more evolute and strongly ribbed. Comparison with *Ch. buckmani* is difficult because this species is known almost entirely from adult macroconchs only; little has so far been seen of the inner whorls. It does however include variants that are much more inflated than the discoidal holotype, so that the identification of the Ipf specimen with *Ch. buckmani* rather than with *Ch. phillipsi* cannot be ruled out on these grounds. The specimen figured by QUENSTEDT also came from the Ipf and could represent the late growth-stages of the one figured here. It differs, however, both from *Ch. phillipsi* and from *Ch. buckmani* in having a less lanceolate whorl-section and less strongly differentiated residual secondary ribbing. The forms from the Ipf may therefore represent yet another transient of *Chamoussetia*, perhaps intermediate in age between *Ch. buckmani* and *Ch. phillipsi*. The specimen figured by CORROY (1932, pl. 11, figs. 3, 4) from Poix, and hence presumed to be of similar age, is also intermediate in morphology.

"*Ch. chamousseti*" was also recorded from the Macrocephalen-Oolith at Erlbach, 20 km NE of the Ipf, by GERSTLAUER (1940, p. 32), and there is a fine phragmocone of diameter 100 mm in the DORN collection in Erlangen from Geyern, near Weissenburg, 30 km E of Erlbach.

4.5. Family Kosmoceratidae HAUG, 1887  
Subfamily Gowericeratinae BUCKMAN, 1926

Genus *Kepplerites* NEUMAYR & UHLIG, 1892  
Subgenus *Gowericeras* BUCKMAN, 1921

*Kepplerites (Gowericeras) densicostatus* TINTANT, 1963  
Pl. 7, fig. 1

1963 *Kepplerites (Gowericeras) gowerianus densicostatus* n. subsp. — TINTANT, p. 141, pl. 15, figs. 1a, b, 2a, b.

cf. 1963 *Kepplerites (Gowericeras) gowerianus* (SOWERBY). — TINTANT partim, p. 121, "population de Poix", pl. 11, figs. 1a–c; pl. 12, fig. 1a, b; pl. 13, figs. 1a, b, 2a, b.

Material: Three adults in situ (SMNS 61624/16, 24, 30) and 2–3 specimens in old collections by matrix; Ipf, bed 5, *macrocephalus* horizon.

Discussion. — The retention of *Gowericeras* as subgenus of *Kepplerites* is arbitrary. It expresses a sudden major change in morphology from the large forms of the Upper Bathonian (see SPATH 1932) — Lower Callovian, *Herveyi* Zone, *Kepplerites* s. s. *keppleri*, to the small forms that reappear, after a faunal gap, in the *K. (G.) toricelli* horizon taken to mark the base of the Koenigi Zone (CALLOMON, DIETL & NIEDERHÖFER 1989, Table 1).

In describing *K. (G.) gowerianus*, TINTANT applied his biometry to a number of heterogeneous assemblages ("populations") arbitrarily assembled from museum material and equally arbitrarily subdivided. His "population de Wiltshire" consisted of a mixture of *K. (G.) metorchus* and *K. (G.) gowerianus* from the English horizons VIII–IX. But he did perceive that the "population de Poix" differed from that of Wiltshire even so, "par l'allure de son ornementation". This is true: the forms from Poix are on the whole more inflated, involute and less serpenticone, the inner whorls more densely and finely ribbed. But instead of assuming the whole assemblage from Poix to be effectively isochronous as he had that from Wiltshire, TINTANT arbitrarily subdivided it into two "subspecies" (sic) on the strength of a single character, the curve of rib-density, singling out about 20% of the sample as *K. (G.) densicostatus*. The differences between the assemblages from Wiltshire and Poix we now know to reflect most probably small differences of age — different faunal horizons.

The specimens from the Ipf best match those from Poix. The one figured in pl. 7, fig. 1 fits almost exactly between TINTANT's holotype (his pl. 15, fig. 1) and paratype (fig. 2).

4.6. Family Tullitidae BUCKMAN, 1921  
Subfamily Bullatimorphitinae nov.

The "bullati" of the Bathonian-Callovian are emerging ever more clearly as important guide-fossils whose closer study is becoming a matter of urgency. Not only do they have a longitudinally world-wide distribution, but locally they show distinguishable faunal successions that have potentially high value for correlation (cf. WESTERMANN & CALLOMON 1988, pp. 14, 78). The family has hitherto incorporated what can now be clearly recognized as two independent lineages, and it is useful to distinguish these at subfamilial level: *Rugiferites* — *Tulites* — (?) *Morrisiceras*: Tullitinae; and *Bullatimorphites* — *Kheraiceras*: Bullatimorphitinae. The earliest known member of the main line is *Bullatimorphites latecentratus* (QUENSTEDT, 1886), from the "Fuscus-Bank" of Laufen, Lower Bathonian, Zigzag Zone, Yeovilensis Subzone.

The latest authenticated record appears to be the curious "*Macrocephalites*" *tuguriensis* (HÉBERT & DESLONGCHAMPS, 1860) from the top Lower Callovian, Enodatum Subzone (CARIOU, 1984, p. 18). A record of an isolated find by HAHN (1971, pl. 7, fig. 4), allegedly from the Upper Callovian, central Swabian Alb, is unreliable. A re-examination of all the evidence in the light of what is now known about the Callovian stratigraphy of the area suggests strongly that the specimen came in fact from the Lower Callovian, Koenigi Zone, *megalocephalus* horizon. The subsidiary lineage of the Tulininae did not survive beyond the Middle Bathonian, Morrisi Zone.

Genus *Bullatimorphites* BUCKMAN, 1921

Subgenus *Kheraicerias* SPATH, 1924

*Bullatimorphites* (*Kheraicerias*) *prahecquensis* (PETITCLERC) [M] and sp. aff.

Pl. 3, fig. 4a, b

1915 *Sphaeroceras prahecquense* PETITCLERC, p. 104, pl. 12, fig. 4 (holotype, mon.).

1984 *Bomburites prahecquense* (PETITC.). — CARIOU, pl. 1, fig. 3a, b.

Material: 1 specimen (sp. s. s.) from bed 6b (*megalocephalus* horizon) and 1 specimen (sp. aff.) from bed 5 (*macrocephalus* horizon).

Description and comparisons. — The specimens from bed 6 and 5 are slightly different and may be regarded as two transients. *B. prahecquensis* differs from its predecessor *B. bullatus* in being smaller and having a more spheroidal, less spindle-shaped phragmocone. The ribbing is finer and denser, persisting on the adult bodychamber. It retains the style of bidichotomous secondary ribbing characteristic of *Kheraicerias* seen also on the inner whorls of the earlier species, to the end of the phragmocone. Adults of *Bull.* (*Kher.*) *prahecquensis* from the *megalocephalus* horizon attain diameters of 55–60 mm, and are now known from the Ipf to the Wutach area. They appear to be identical with the type assemblage: we are indebted to Dr. CARIOU for casts of a topotype and a chorotype from Pamproux. The species illustrated here is a slightly younger transient from the *macrocephalus* horizon.

#### Acknowledgments

It gives us pleasure to acknowledge the help we have received from many sources. We are indebted to M. Kapitzke and M. Rieter (Stuttgart) for their enthusiastic participation in the excavations and for the preparation of the collections, and H.-E. Haehl † (Stuttgart) for the photography of the plates. We thank V. Dietze, U. Sauerborn and H. Hager (Aalen) for information and for placing some important specimens in their collections at our disposal, and the ladies G. and U. Schwarz (Bopfingen-Oberdorf) for generously donating a part of the collection of their father, D. Schwarz, to the Staatliches Museum für Naturkunde Stuttgart. Dr. M. K. Howarth, London, kindly provided us with casts of the type of Sowerby's *Amm. herveyi* in the Natural History Museum (London). Dr. M. Warth, Stuttgart, gave us information about historical maps. Dr. A. Liebau, Tübingen, allowed us to study some specimens of the Quenstedt type-collection.

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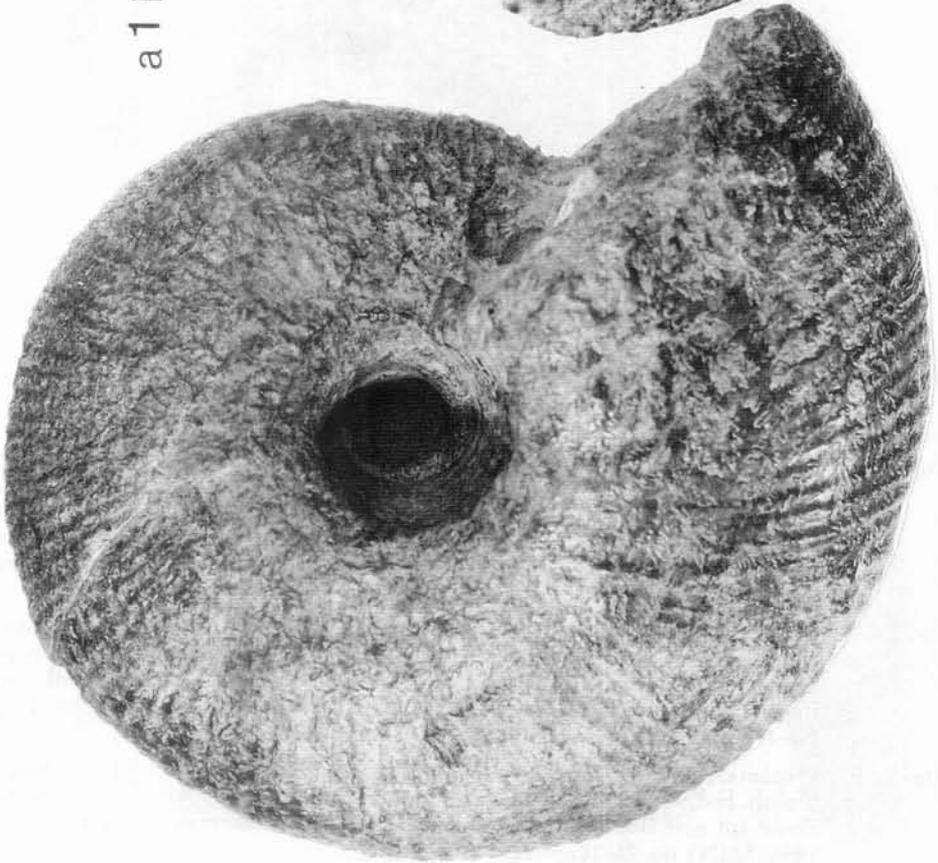
Dipl.-Geol. H.-J. Niederhöfer, Staatliches Museum für Naturkunde, Rosenstein 1, D-7000 Stuttgart.

## Plate 1

Fig. 1a, b. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], phragmocone; Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; Blasienberg near Kirchheim am Ries, eastern Swabian Alb, SW-Germany; coll. D. Schwarz 1982; SMNS no. 61625. — x1.

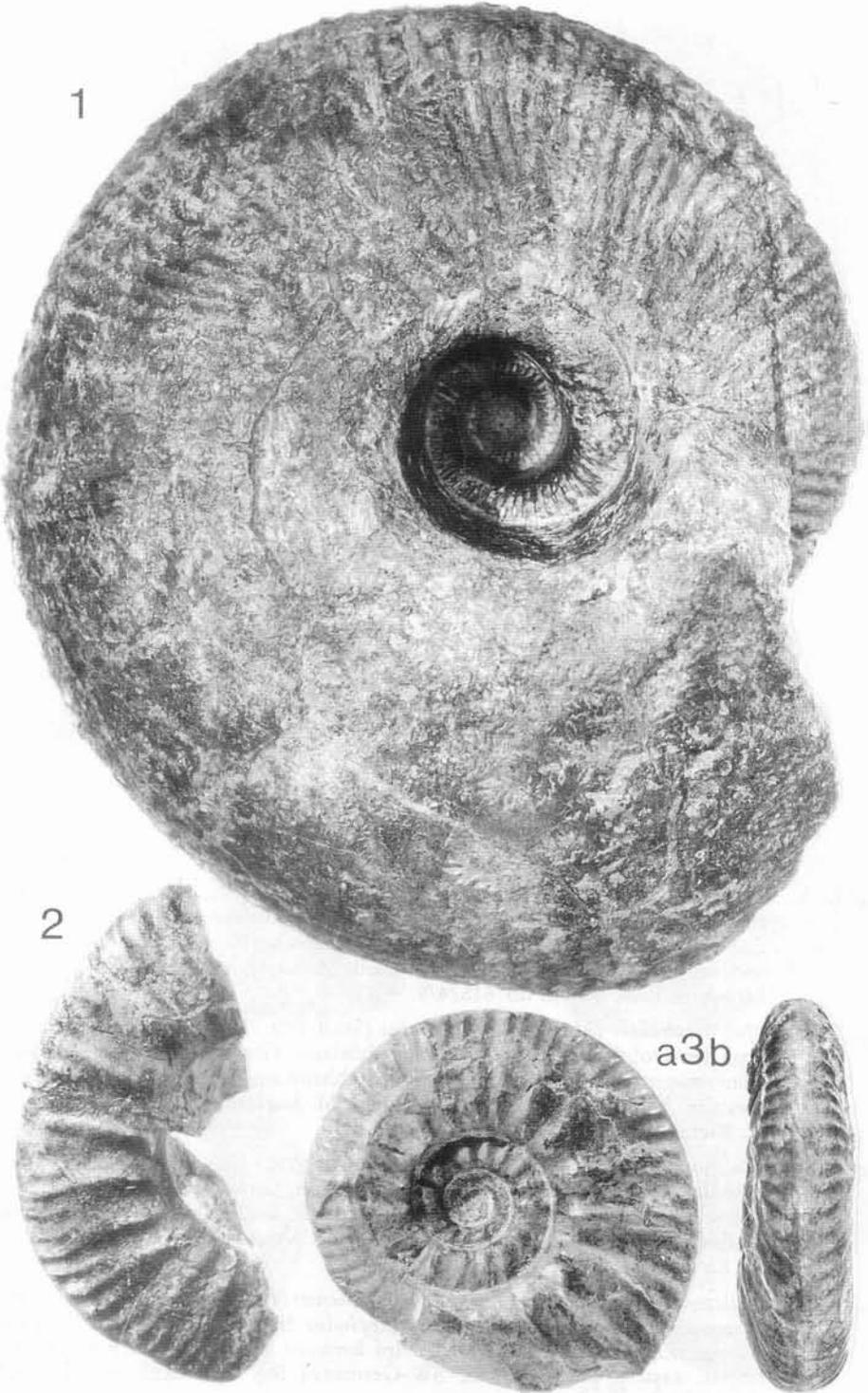


a1b



## Plate 2

- Fig. 1. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], phragmocone with beginning of bodychamber; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/12. — x1.
- Fig. 2. *Proplanulites (Propl.) cf. subcuneiformis* BUCKM. [m], fragment of bodychamber; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/51. — x1.
- Fig. 3a, b. *Proplanulites (Propl.) cf. fabricatus* (BUCKM.) [m], inner whorls; Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; Ipf near Bopfingen, eastern Swabian Alb, SW-Germany; coll. E. Köstlin 1966; SMNS no. 28710. — x1.



## Plate 3

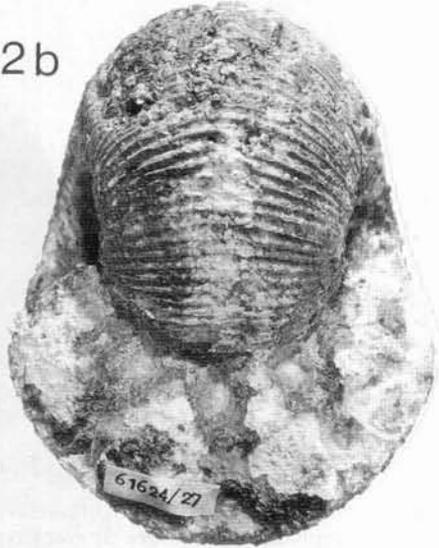
- Fig. 1a, b. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], inner whorls; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/8. — x1.
- Fig. 2a, b. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], inner whorls; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/27. — x1.
- Fig. 3. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], inner whorls; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/21. — x1.
- Fig. 4a, b. *Bullatimorphites (Kheraicerias) aff. prahecuensis* (PETITCL.) [M], adult specimen; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. H. Hager, Aalen; SMNS no. 61624/23. — x1.



a1b



a2b



3

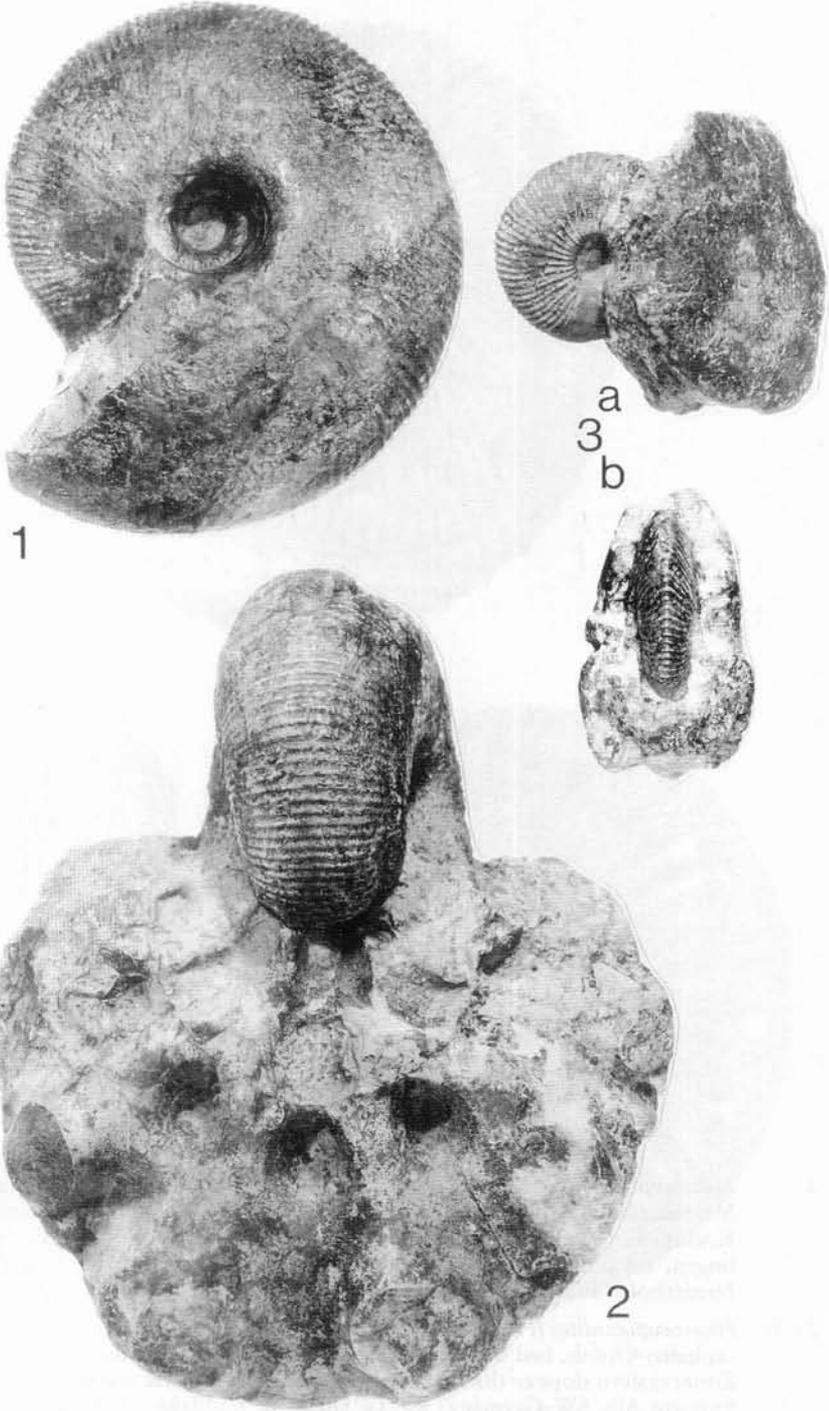


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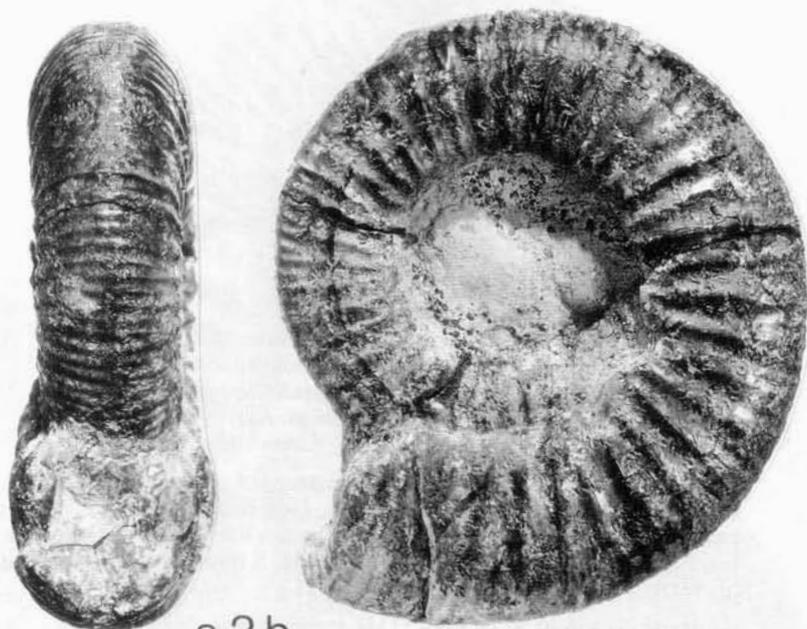
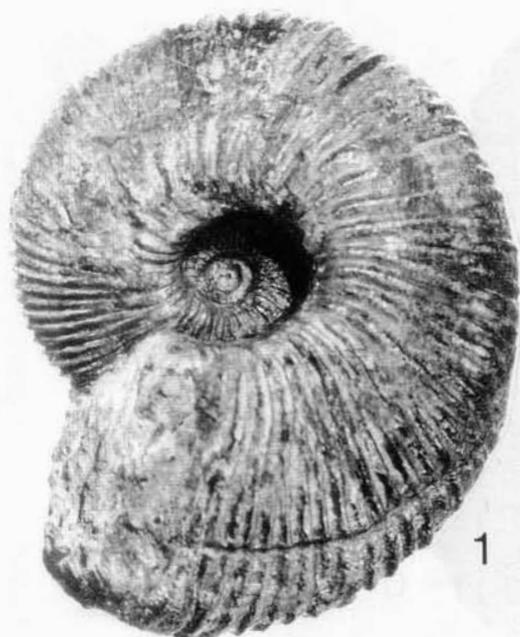
## Plate 4

- Fig. 1. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], phragmocone; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/29. — x1/2.
- Fig. 2. *Macrocephalites (Macr.) macrocephalus* (SCHLOTH.) [M], compared with the outer whorl the inner whorls are compressed; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/7. — x1.
- Fig. 3a, b. *Chamoussetia* cf. or aff. *phillipsi* CALLOMON & WRIGHT [M], phragmocone; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/14. — x1.



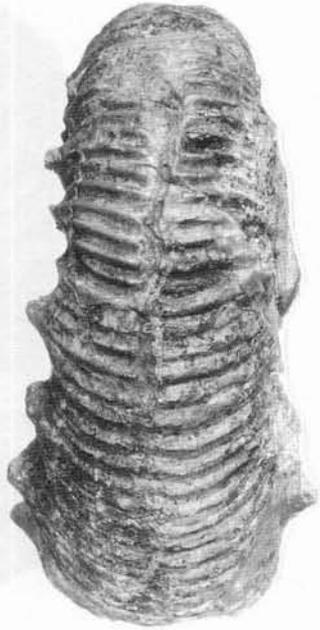
## Plate 5

- Fig. 1. *Macrocephalites (Pleurocephalites) aff. folliformis* BUCKM. [m], adult specimen; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/28. — x1.
- Fig. 2a, b. *Homoeoplanulites (Parachoffatia) aff. funatus* (OPPEL) [M], inner whorls; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/18. — x1.

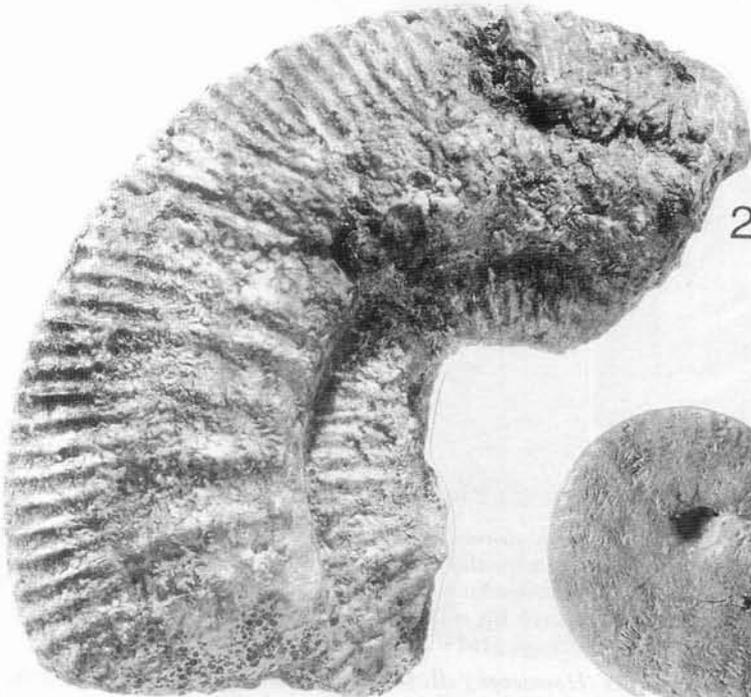


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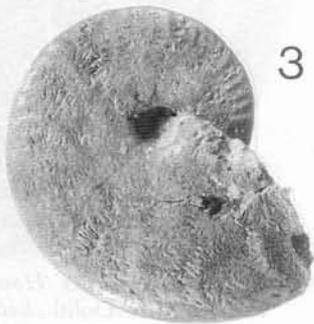
- Fig. 1a, b. *Reineckeia quenstedti* nom. nov. pro *R. franconica* (QUENST. non SCHLOTH.) [M], juvenile specimen; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/19. — x1.
- Fig. 2. *Reineckeia grossouvrei* PETITCL. [M], fragment of phragmocone; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/52. — x1.
- Fig. 3. *Paroxycerites subdiscus* (D'ORB.) [M], inner whorls; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen; eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/53. — x1.



a1b



2



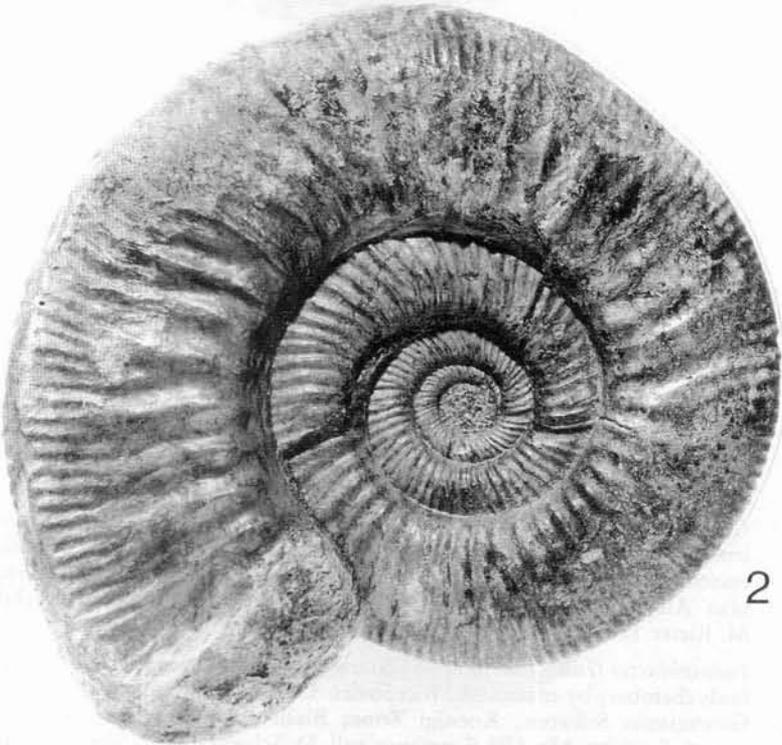
3

## Plate 7

- Fig. 1. *Keplerites (Gowericeras) densicostatus* TINT. [M], adult specimen; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/24. — x1.
- Fig. 2. *Homoeoplanulites (Homoeopl.) aff. furculus* (NEUM.) [m], adult specimen; Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; Blasienberg near Kirchheim am Ries, eastern Swabian Alb, SW-Germany; coll. D. Schwarz 1982; SMNS no. 61678. — x1.



1



2

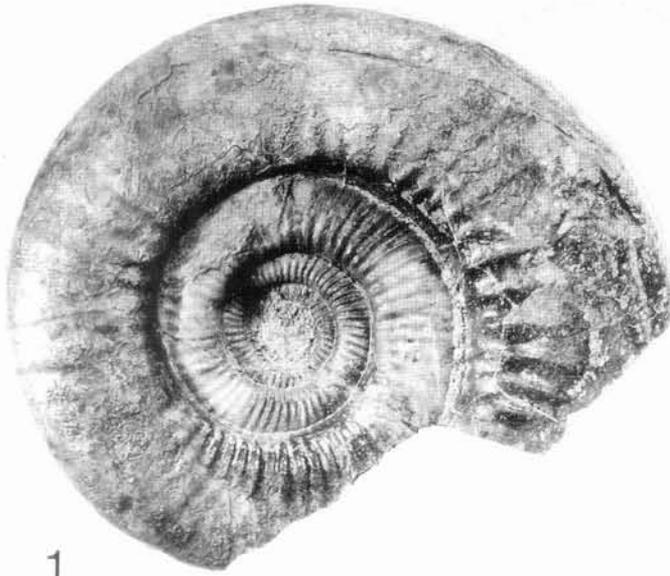
## Plate 8

- Fig. 1. *Choffatia (Subgrossowria) recuperoi* (GEMM.) [M], phragmocone; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/6. — x1/2.
- Fig. 2. *Indosphinctes (Ind.)* aff. *spirorbis* (NEUM.) [M], adult specimen with beginning of bodychamber; by matrix Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; Blasienberg near Kirchheim am Ries, eastern Swabian Alb, SW-Germany; coll. D. Schwarz 1982; SMNS no. 61626. — x1/2.



## Plate 9

- Fig. 1. *Indosphinctes (Ind.)* nov. sp. [M]; Macrocephalen-Oolith, bed 5, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; eastern slope of the Ipf between Kirchheim am Ries and Bopfingen, eastern Swabian Alb, SW-Germany; leg. G. Dietl, M. Kapitzke, H.-J. Niederhöfer and M. Rieter 1986; SMNS no. 61624/3. — x1/2.
- Fig. 2. *Proplanulites (Crassiplanulites) basileus* BUCKM. [M]; phragmocone of an adult specimen; Macrocephalen-Oolith, bed 5 by matrix, *macrocephalus* horizon, Gowerianus Subzone, Koenigi Zone; Ipf near Bopfingen, eastern Swabian Alb, SW-Germany; old coll.; SMNS no. 61952. — x1/2.



1



2

## Plate 10

- Fig. 1. *Choffatia (Subgrossowria) recuperoi* (GEMM.) – specimen of pl. 8, fig. 1.  
Fig. 2. *Reineckeia grossowvrei* PETITCL. – specimen of pl. 6, fig. 2.  
Fig. 3. *Homoeoplanulites (Homoeopl.) aff. furculus* (NEUM.) – specimen of pl. 7, fig. 2.  
Fig. 4. *Indosphinctes (Ind.)* nov. sp. – specimen of pl. 9, fig. 1.  
Fig. 5. *Proplanulites (Crassiplanulites) basileus* BUCKM. – specimen of pl. 9, fig. 2.  
Fig. 6. *Indosphinctes (Ind.) aff. spirorbis* (NEUM.) – specimen of pl. 8, fig. 2.  
All figures 1:1.

