New internally structured decapod microcoprolites from Germany (Late Triassic/Early Miocene), Southern Spain (Early/Middle Jurassic) and Portugal (Late Jurassic): Taxonomy, palaeoecology and evolutionary implications

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With 12 figures and 1 table

Kurzfassung: Internstrukturierte fossile Kotpillen werden zum ersten Mal aus nichtmarinen Milieus beschrieben. In den lakustrinen Lehrberg-Schichten des Mittleren Keupers (Karnium) kann der älteste bisher bekannte Vertreter der Formgattung *Helicerina* BRÖNNIMANN & MASSE in Gestalt der neuen Art *H. keuperina* SEEGIS n. sp. nachgewiesen werden. *Favreina kalankyra* EBLI aus dem norischen Hauptdolomit wird ebenfalls zu *Helicerina* gestellt. Aus einem untermiozänen Süßwasserkalk Süddeutschlands wird die neue Koprolithen-Art *Helicerina ruttei* SCHWEIGERT n. sp. aufgestellt. Diese Art läßt sich auf die an demselben Fundort verbreitete Süßwasserkrabbe *Proballaya quenstedti* (ZITTEL) beziehen. Koprolithen der Gattung *Helicerina* stammen deswegen sicher nicht von den Anomuren, sondern von brachyuren Decapoden bzw. deren triassischen Vorläufern.

Weitere Decapoden-Koprolithen werden aus pelagischen, eisenreichen Kalken des subbetischen Juras von Südspanien beschrieben. Neben *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO und der bekannteren Art *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI wird die neue Art *Favreina belandoi* FELS n. sp. beschrieben. Sie zeichnet sich durch eine variierende Anzahl von Kanälen aus, die sich auf verschiedene ontogenetische Stadien des produzierenden Krebses beziehen lassen.

Aus dem oberjurassischen Ota-Kalk Portugals wird *F. prusensis* (PARÉJAS) sowie die damit zusammen vorkommende neue Art *Petalina hexalunulata* LEINFELDER n. gen. n. sp. beschrieben. Die neue Formgattung *Petalina* unterscheidet sich von *Favreina* durch halbkreisförmige Kanalquerschnitte. In Portugal sind beide Arten auf intrajurassische marine Karstspalten-Füllungen innerhalb des Ota-Riffkalks beschränkt.

Abstract: Fossil faecal pellets with internal structures are described from non-marine environments for the first time. In the Late Triassic Lehrberg Beds (Middle Keuper, Carnian) of Germany, the oldest stratigraphic record of the form genus *Helicerina* BRÖNNIMANN & MASSE, *Helicerina keuperina* SEEGIS n. sp., occurs. *Favreina kalankyra* EBLI from the Norian Hauptdolomit Formation is also attributed to this genus. Another new species of *Helicerina*, *H. ruttei* SCHWEIGERT n. sp., is described from the Early Miocene calcareous freshwater tufas of Southern Germany. It is attributed to the brachyuran freshwater crab *Proballaya quenstedti* (ZITTEL) which occurs abundantly at the same locality. Hence, the coprolite genus *Helicerina* is the product of brachyuran decapods or their Triassic ancestors, and not of anomuran decapods as thought before.

From younger Early to Middle Jurassic pelagic ferrugineous limestones of the Subbetic area (Southern Spain), the new species *Favreina belandoi* FELS n. sp. is described besides *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO, and the better known species *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI. The number of canals within *Favreina belandoi* varies but is clearly correlated with different ontogenetic stages of the same producer.

From the Late Jurassic of Portugal, the new species *Petalina hexalunulata* LEINFELDER n. gen. n. sp. is reported. It co-occurs with *Favreina prusensis* (PARÉJAS). The new genus *Petalina* is distinct from *Favreina* by its hemispherical cross sections of the canals. In Portugal, both species are restricted to intrajurassic marine karstic fissures of the reefal Ota Limestone.

Preface

In the last few years a lot of papers dealing with crustacean microcoprolites have been published so that the number of known species has rapidly increased. In Stuttgart, during microfacies investigations of carbonates which differ widely in age and geographic setting (Fig. 1), a number of further microcoprolites have been found, some completely new, some of them recorded for the first time from a special region. We decided to describe them together, because all of our observations led to several comprehensive approaches on systematics, ontogenetic evolution, biostratigraphic value, and palaeoecology of crustacean microcoprolites.

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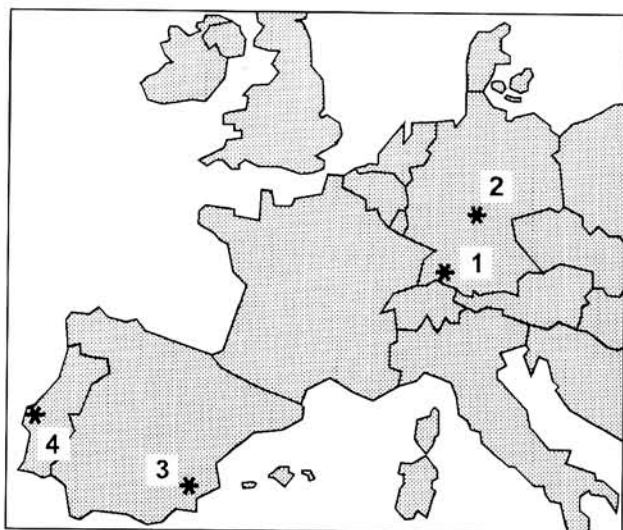
Fig. 1. Localities of the investigated samples. – 1: Engelswies (Early Miocene, Germany), 2: Eschwege (Late Triassic, Germany), 3: Sierra del Reclot (Early to Middle Jurassic, Spain), 4: Alenquer (Late Jurassic, Portugal).

Microcoprolites and their producers from the Early Miocene of Southern Germany

(G. SCHWEIGERT)

At the southern margin of the Swabian Alb (Southern Germany) freshwater algal tufas of Miocene age have been quarried near the little village of Engelswies (RUTTE 1953, 1954). Today the outcrops are protected as a natural monument. The locality is well known because of its abundant fossil mammal remains and imprints of plants. The fossil macroflora has been described by SCHWEIGERT (1992), whereas the micromammal fauna has been recently investigated by ZIEGLER (1995). According to the latter, the freshwater tufas can be dated as Early Miocene (MN 5) in age.

Microscopic investigations of the lithofacies showed that in some horizons internally structured crustacean microcoprolites represent a rockforming component within the freshwater tufas of Engelswies (SCHWEIGERT 1996). In many cases, it is however difficult to recognize them as microcoprolites because the rocks are altered by recristallisation and diagenetic leaching processes caused by plant rootlets. Other microcoprolites are disintegrated into peloidal clots which are no longer distinguishable from peloids of microbial origin. This is not astonishing, because modern crustacean microcoprolites exhibit large amounts of undigested plant debris (PRYOR 1975).

The tufas of Engelswies are the only known locality which yielded numerous fossil freshwater crabs apart from similar tufas of Pliocene age in the Esztergom and Komárom district of northern Hungary (LÖRENTHEY & BEURLEN 1929: 232). According to our knowledge the microfacies of the Hungarian tufas has not been investigated so far.

Systematics

According to VIALOV (1978), we agree that it is better to treat crustacean microcoprolites as ichnofossils, and hence we use ichnotaxa for crustacean microcoprolites, because the systematic position of their producers must remain doubtful in most cases with only very few exceptions.

Favreinidae VIALOV 1978
Helicerina BRÖNNIMANN & MASSE 1968

Type species: *H. spinosa* BRÖNNIMANN & MASSE 1968.

Up to the present, only four species of microcoprolites have been placed in the genus *Helicerina*: *H. spinosa* BRÖNNIMANN & MASSE 1968, *H. alata* BRÖNNIMANN & MASSE 1968, *H. siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO 1979, and *H. kainachensis* FENNINGER & HUBMANN 1994. In this paper two additional species, *H. keuperina* SEEGIS n. sp. and *H. ruttei* SCHWEIGERT n. sp., are described. *Favreina kalankyra* EBLI 1990 from the Norian of the Northern Alps is now also attributed to *Helicerina* (see Fig. 5), because of its similarity to other *Helicerina* species and its canals within the symmetry plane.

Emended diagnosis: The form genus *Helicerina* is characterized by triangular or diamond-shaped canals within the symmetry plane of cross sections. Laterally, rounded shaped canals can develop from spine-like extensions of the central canals on each side of the symmetry plane.

Helicerina ruttei n. sp.
Fig. 2 a-h

1996 *Helicerina* n. sp. – SCHWEIGERT: fig. 21.

Derivatio nominis: dedicated to Prof. Dr. E. RUTTE (formerly University of Würzburg) who described the algal tufas of Engelswies (RUTTE 1953, 1954).
Holotype: the specimen figured on Fig. 2a; the thin section is housed in the Staatliches Museum für Naturkunde Stuttgart (SMNS 62625).
Locus typicus: Talsberg, 1 km west of the village of Engelswies near Meßkirch, Baden-Württemberg, SW Germany.
Stratum typicum: Calcareous tufas at the base of the Upper Freshwater Molasse, Early Miocene, Karpatian, Neogene mammal unit MN 5.

Diagnosis: Species of the genus *Helicerina* with three canals in the symmetry plane. The ventral and middle canal of which are interconnected both with two lateral canals by "interconnected lines".

Description: The microcoprolites have an average diameter of 0.39 mm. They normally exhibit 11 canals and a pronounced "dorsal" groove. Three of the canals have an angular shape. They are positioned in the symmetry plane, and are connected with each other and with the dorsal groove by "interconnecting lines". Some small

specimens yield only two canals in the symmetry plane, and then the "dorsal" canal is missing. The central and the ventral canals are both laterally connected with two pairs of probably round-shaped canals. The length of the microcoprolites varies; it averages around 0.9 mm.

Discussion: Most similar to *H. ruttei* n. sp. is *Helicerina kainachensis* FENNINGER & HUBMANN from the Late Cretaceous of the Kainach Basin (Austria). The latter differs from *H. ruttei* by the occurrence of three lateral canals connected with the central canal in the symmetry plane. The ventral canal is described to be connected with only one lateral canal, but the photographs led to the conclusion, that in reality the lateral canal consists of a pair of canals as it is the case in *H. ruttei*. This lateral pair of canals has a different orientation in both species.

Interestingly the diagnosis of *Favreina kalankyra* given by EBLI (1990) fits also perfectly with *Helicerina ruttei*

although the arrangement of canals within both species is clearly totally different.

The producer of *Helicerina ruttei*

Up to date, all internal structured fossil crustacean microcoprolites have been considered as the product of marine anomuran decapods in analogy with a few modern investigations (e.g. MOORE 1932). In the past, most of the microcoprolites were attributed to thalassinoid decapods, and only the form genus *Thoronetia* with its ventral "cap" was said to be the product of galatheid decapods (BRÖNNIMANN 1972; FÖRSTER 1977). KENNEDY et al. (1969) erroneously related anomuran crustaceans (e.g. *Mecochirus*) which were found together with internally structured microcoprolites to the Brachyura. In most cases, however, the producer of the microcoprolites remained unknown. FÖRSTER & VON HILLEBRANDT (1984) described
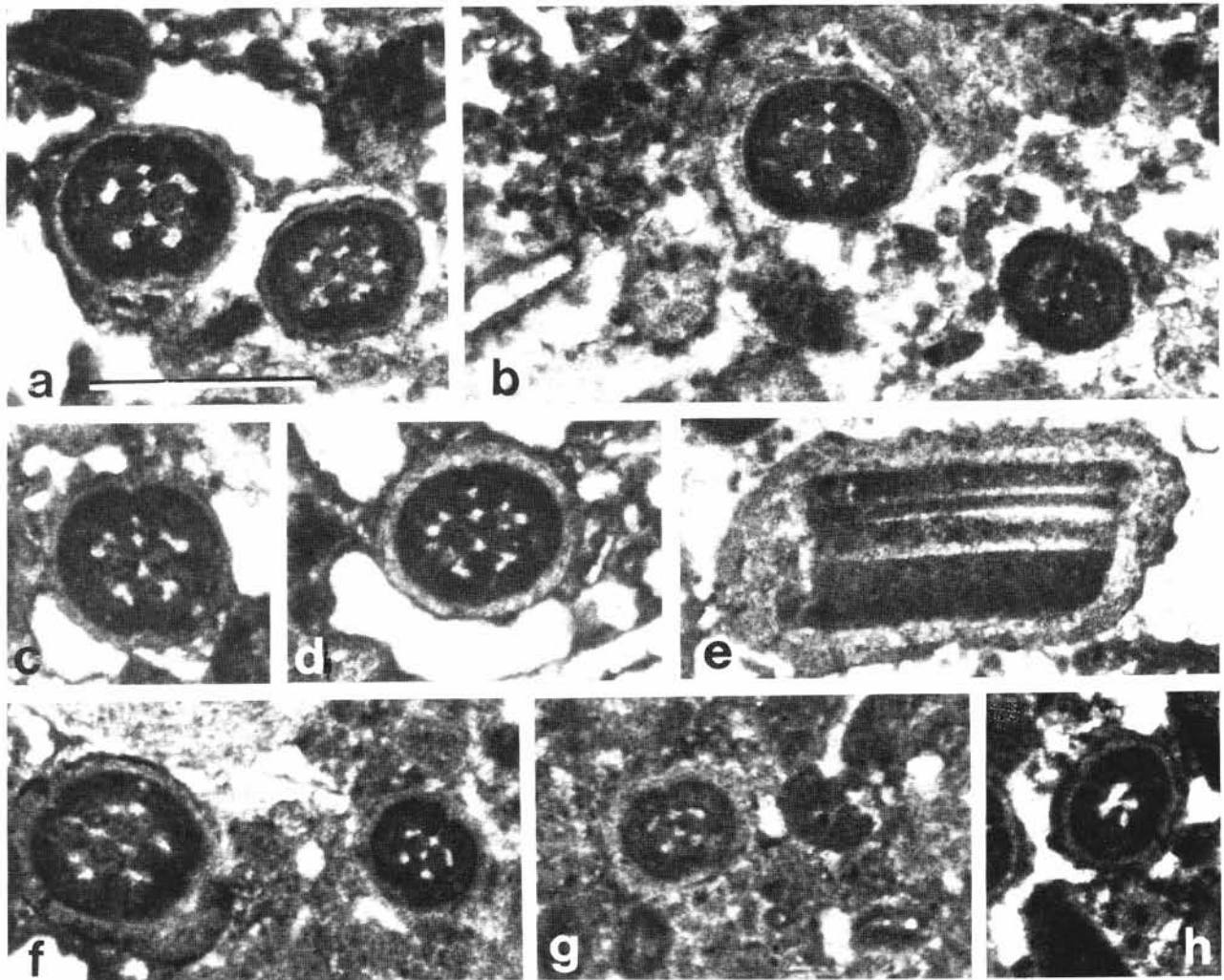

Fig. 2. *Helicerina ruttei* SCHWEIGERT n. sp. – Early Miocene freshwater tufas of Engelswies (SW Germany). Thin section no. SMNS 62625. – Scale bar: 1 mm.
a: Holotype specimen (at the left); **b-d:** additional specimens in cross section; **e:** longitudinal section of a small microbial onkoid around *H. ruttei*; **f-g:** cross sections of very small specimens showing only 2 canals in the symmetry plane; **h:** cross section of a pathologic specimen.

microcoprolites of the form genus *Favreina* associated with the thalassinid *Mecochirus* from the Late Jurassic of Northern Chile. In the calcareous tufas of Engelswies, a freshwater crab is extremely common, and it is the only decapod species of this locality. For that reason it is evident that this crab must have been the producer of the microcoprolites of the ichnospecies *Helicerina ruttei*.

Systematic position of the freshwater crabs of Engelswies

Phylum Arthropoda SIEBOLD & STANNIUS 1845
Class Malacostraca LATREILLE 1806
Order Decapoda LATREILLE 1803
Suborder Brachyura LATREILLE 1803
Family Potamidae ORTMANN 1896

Genus *Proballaya* BOTT 1955

Proballaya quenstedti (ZITTEL 1885)
Fig. 3 a-f

v   1885 *Telphusa speciosa* – QUENSTEDT: 400, pl. 31, figs. 5-8.
v * 1885 *Telphusa Quenstedti* – ZITTEL: 715.
v   1929a *Potamon quenstedti* (ZITTEL), 1885 – GLAESSNER: 338 [synonyms up to that date].
v   1929b *Potamon quenstedti* (ZITTEL) – GLAESSNER: 54, pl. 6, figs. 4-5.
v   1930 *Potamon quenstedti* (ZITTEL) – GLAESSNER: 169, pl. 8, fig. 5; pl. 9, fig. 5; pl. 10, fig. 2.
v   1935 *Potamon quenstedti* – ABEL: 360.
v   1955 *Proballaya quenstedti* – BOTT: 310.
v   1969 *Proballaya quenstedti* – BOTT: 271.
v   1996 *Proballaya quenstedti* (ZITTEL) – SCHWEIGERT: fig. 22.

Lectotype: QUENSTEDT 1885: pl. 31, fig. 5, housed in Tübingen (GPIT), refigured herein (Fig. 3a-c).
Stratum typicum: Calcareous tufas at the base of the Upper Freshwater Molasse, Early Miocene, Karpatian, Neogene mammal unit MN 5.
Occurrence: Very frequent in the freshwater tufas of Engelswies near Sigmaringen; one single claw from Langenenslingen near Riedlingen (SMNS 62534/2).

For a long time after their discovery by O. FRAAS (1865), the crabs of Engelswies were thought to be identical with *Thelphusa speciosa*, a freshwater crab which was originally described from the celebrated Late Miocene fossiliferous Öhningen limestones (VON MEYER 1862). The latter is the type species of the monospecific genus *Propotamonautes* (BOTT 1955: 310). ZITTEL (1885) established a new species, *Telphusa quenstedti*, based on the specimens from Engelswies figured by QUENSTEDT (1885). In ENGEL (1908) both species, *Telphusa speciosa* and *Telphusa quenstedti*, are mentioned in a fossil list of the tufas, but both quotations are based on identical specimens. GLAESSNER (1930) reinvestigated the type material from Öhningen and from Engelswies and concluded both species being different from each other. Interestingly, the crabs from Engelswies have been thought to have morphological affinities to extent African freshwater crabs. This opinion, however, was only based on the figures of QUENSTEDT, and already GLAESSNER stated that there are much more affinities to the modern European freshwater crab *Potamon fluviatile*. Obviously the paper of GLAESSNER was unknown to BOTT (1955, 1969), who again tried to focus on morphological affinities with modern African Potamonautidae, especially with *Potamonautes ballayi*.
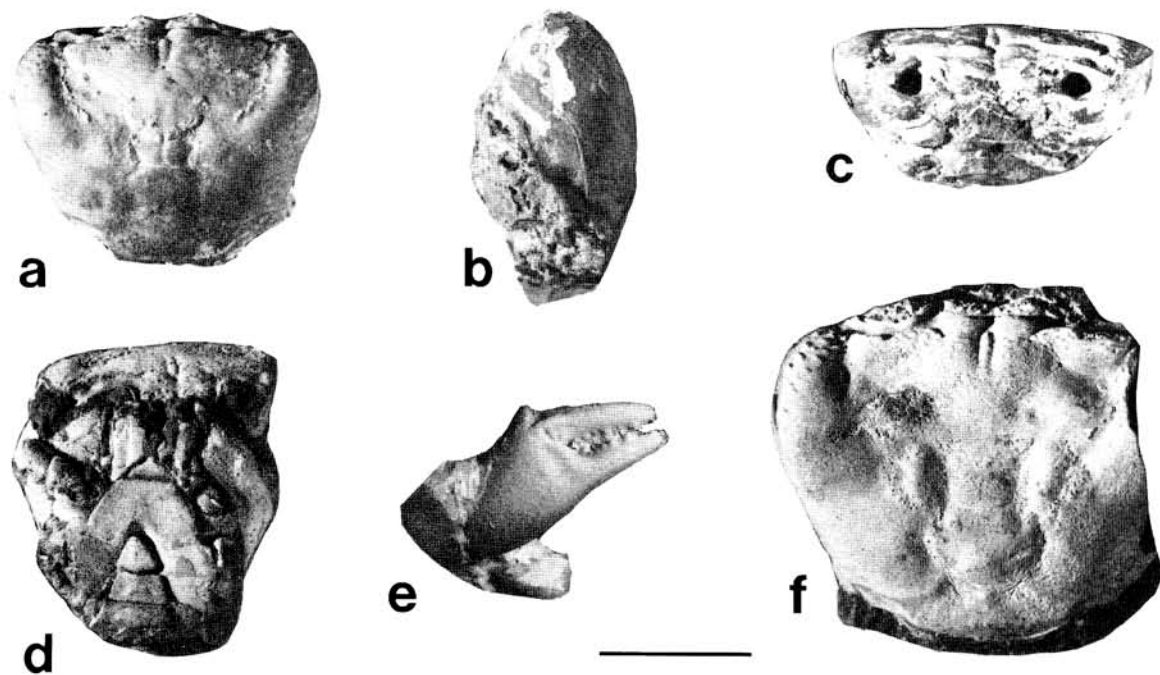

Fig. 3. *Proballaya quenstedti* (ZITTEL). – Early Miocene (Karpatian, MN 5) freshwater tufas of Engelswies. – Scale bar: 2 cm. **a-c:** lectotype, figured by QUENSTEDT 1885: pl. 31, fig. 8; **d:** specimen figured by GLAESSNER (1929b: pl. 6, fig. 4-5), SMNS 4782 (collection O. FRAAS); **e:** silicon cast of a right hand, SMNS 62534/1 (collection G. SCHWEIGERT); **f:** specimen figured by GLAESSNER (1930: pl. 8, fig. 5), SMNS 4758 (collection O. FRAAS).

He argued that the specimens figured by QUENSTEDT show the presence of a postfrontal crista running from one edge of the carapax to the other without any interruptions, as it was found to be typical of modern African Potamonautidae. For that reason BOTT (1955) created the new genus *Proballaya*. Based on these data PRETZMANN (1987) postulated an early immigration of African freshwater crabs to Europe during the Miocene, and a later immigration of modern freshwater crabs from the eastern Mediterranean area and from Asia.

However, the drawing of the lectotype in QUENSTEDT (1885) is somewhat simplified, especially what concerns the development of the postfrontal crista. A refiguration of the lectotype (Fig. 3a) and of an additional larger specimen (Fig. 3f) clearly demonstrates that the postfrontal crista exhibits distinct gaps on both sides of the carapax, as it is typical of European and Asian freshwater crabs. Especially the genera *Potamon*, *Malayopotamon* and *Stoliczia* are very similar to *Proballaya*. For example, it is nearly impossible to distinguish morphologically between the modern *Stolizcia goal* from Malaysia, recently described by NG (1993), and the fossil crab *Proballaya quenstedti* (ZITTEL), which, according to the age determinations based on micromammal stratigraphy, represents the oldest known freshwater crab. Not only the carapax but also the shape of the maxillipeds, which are visible at a well preserved exuvie specimen described by GLAESSNER (1929b, refigured here Fig. 3d), appears very similar, and only the teeth of the claws are different in both species. Hence, *Proballaya quenstedti* does certainly not derive from African ancestors. In the Holocene, an enormous radiation has started in freshwater crabs. Numerous species were described especially from tropical Asian rivers (PRETZMANN 1962; BOTT 1970a, b), and also the only European species *Potamon fluviatile* is now subdivided into different geographic subspecies (PRETZMANN 1990). In our opinion the same adaption to local environmental conditions took part in Miocene times, and hence *Proballaya quenstedti* is considered to be endemic in the brackish sea of the Molasse basin of Southern Germany. Its unknown ancestor might have been a marine crab which lived in the same area in the older "Obere Meeresmolasse" marine seaway.

Microcoprolites from the Lehrberg Beds of the Middle Keuper (D.B. SEEGIS)

Helicerina keuperina SEEGIS n. sp.
Figs. 4a-f, 5

Derivatio nominis: after the occurrence in the Keuper.
Holotype: specimen figured on Fig. 4a below the fragmentary specimen; the thin section is housed at the Staatliches Museum für Naturkunde Stuttgart (SMNS 62626/1).
Paratypes: specimens illustrated on Fig. 4b, c, e, f.
Locus typicus: Lengröden SE Eschwege, farmland north of the village; TK 25 4927 Creuzburg. R 35 88 380, H 56 55 560; see VON FRITSCH (1870: 388), NAUMANN (1907: 39; 1910: 562).
Stratum typicum: Upper part of the Lower Lehrbergbank; Waldenburg Subgroup of the Löwenstein-Group, Middle Keuper.

Diagnosis: A species of the form genus *Helicerina*, showing the following characters: faecal pellets rounded in cross section. Width 0.25-1.7 mm. Canal system consisting of a central part with three pairs of lateral appendices; the upper and middle pair branches from the central canal, the lower pair from the middle pair of appendices. Dorsally, the canal system has a narrow connection to the surface of the pellet.

Description: The diameter ranges between 0.25 and 1.7 mm, 0.4-0.6 mm being the most frequent values. The length is between 0.3 and 3 mm, with two slight maxima at 0.4-0.5 and 0.8-0.9 mm. In cross section, a bilaterally symmetric canal system is developed, consisting of a central part with three projections on either side. According to the terminology of FENNINGER & HUBMANN (1994), the following elements can be distinguished from dorsal to ventral: a single dorsal canal, running in a longitudinal direction and establishing the connection to the surface of the pellet; two median canals, each one with a pair of lateral canals, the upper pair having a lateral, the lower pair an obliquely downward direction; two paired, vertically oriented basal canals, branching from the second pair of lateral canals.

In longitudinal section, a central cavity filled by sediment or – in specimens showing a rather tangential section – one to three longitudinal canals can be observed. It seems that the central part of the canal system was particularly susceptible to decomposition. Indications for this are the very different width and distinctness of the canals in different faecal pellets. During decomposition, a broadening and extension of the median canal took place, so that in cross section the lateral and basal canals appear only as short projections of this median canal. At advanced decomposition, the canal system turned into a broad cavity which could be filled with micrite and detrital quartz grains of the surrounding sediment. A few specimens (e.g. Fig. 4d) show delicate lines running normally to obliquely to the long axis of the coprolite.

Preservation: All specimens consist of fine-grained dolomicrite. The very early dolomitisation in the Lehrbergbänke (SEEGIS 1996) is responsible for the good preservation even of delicate sedimentary structures. In reflected light, most specimens can be identified readily by their white color. In transmitted light, they appear dark, depending on the small grain size of the dolomicrite. The best preservation is found at the type locality. The specimens from southern Germany often show only a slight contrast in relation to the surrounding matrix and can be observed most easily in polished sections.

Relations: The new species is closest to *H. siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO 1979, which possesses only four laterally directed projections branching from a median canal. *H. spinosa* BRÖNNIMANN & MASSE 1968, shows only two lateral canals, branching from a median canal. *H. kainachensis* FENNINGER & HUBMANN 1994, *H. ruttei* SCHWEIGERT (this paper) and
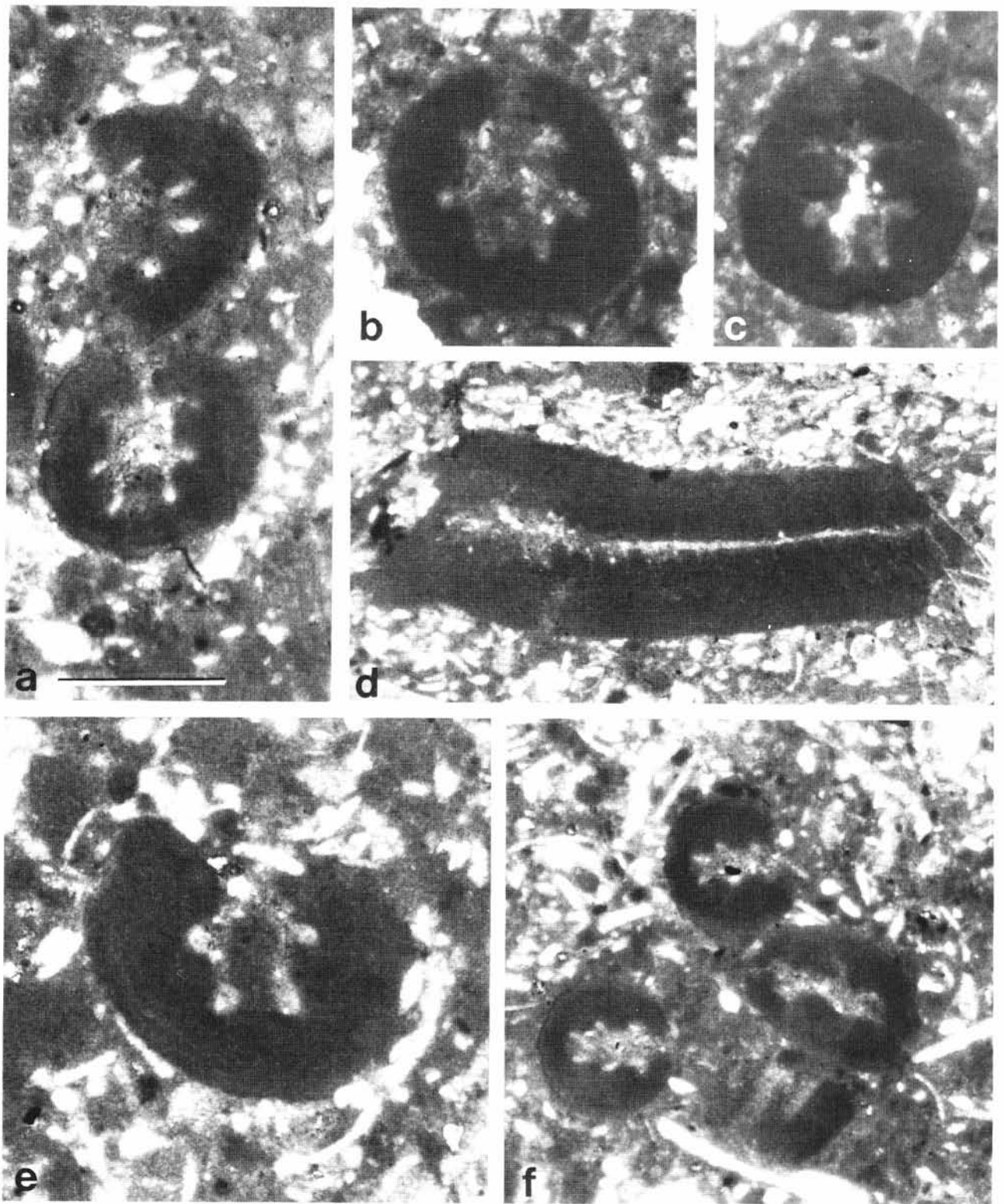
Fig. 4. *Helicerina keuperina* SEEGIS n. sp.- Lengröden. SE of Eschwege. Middle Keuper. Lehrberg Beds. upper part of the Lower Lehrbergbank.
a: holotype (lower specimen). cross section. (thin section SMNS 62626/1); **b-c, e, f:** paratypes (b: SMNS 62626/8; c: SMNS 62626/5; e: SMNS 62626/1; f: SMNS 62626/1); **d:** longitudinal section showing the stages of infill (SMNS 62626/10). – Scale bar: a-c. e-f = 0.5 mm; d = 0.25 mm.
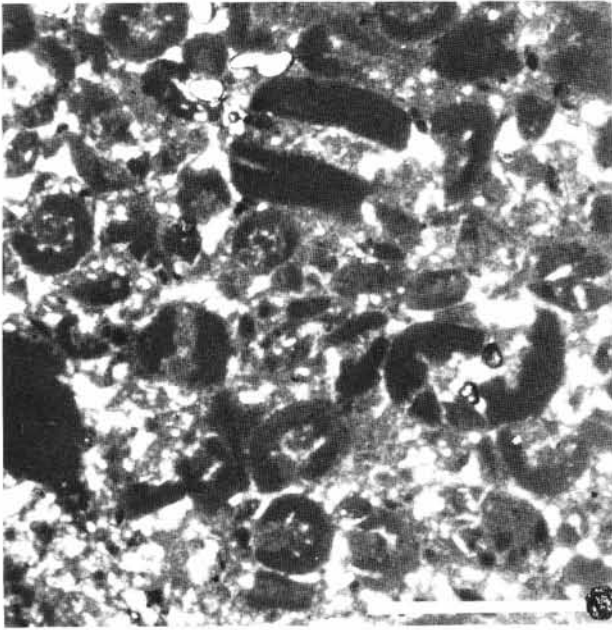
Fig. 5. *Helicerina keuperina* SEEGIS n. sp. – Lengröden, SE of Eschwege, Middle Keuper, Lehrberg Beds, upper part of the Lower Lehrbergbank. – Partly disintegrated specimens (thin section SMNS 62626/5). – Scale bar: 0.25 mm.

H. kalankyra (EBLI 1990) have more canals which are separated from each other clearly and are connected only by narrow interconnecting lines (for comparison see Fig. 6!).

Stratigraphy: The Lehrberg Beds of the Middle Keuper are widely distributed in southern Germany, in the Weserbergland, the Leinetal, near Eschwege and in Thuringia (Fig. 7). They consist of a few metres of alternating red, green and violet clay- and marlstones with intercalated dolomitic carbonate layers which are called Lehrbergbänke. The latter reach up to a few decimetres in thickness and are – in contrast to the almost completely unfossiliferous claystones – in most cases fossiliferous. Usually, three Lehrbergbänke are developed; they are termed Lower, Middle and Upper Lehrbergbank (THÜRACH 1888/89). Recent investigations (SEEGIS 1996) showed that the Lower Lehrbergbank must be subdivided stratigraphically into two units which are separated by a small hiatus and which are mainly characterized by a different faunal content.

Each Lehrbergbank is characterized by its own faunal assemblage; furthermore, some regional faunal differences have been observed (SEEGIS, in prep.). Towards the southern and eastern basin margins, the Lehrberg Beds are replaced increasingly by fluvial sandstones (Kiesel- and Blasensandstein).

H. keuperina represents the first record of a crustacean coprolite in the German Upper Triassic. According to vertebrate data, the Lehrberg Beds are very probably Late Carnian in age (WILD 1990: 15; SEEGIS 1996); therefore, *H. keuperina* is the oldest known species of this genus. *H. siciliana* originally described from marine Norian sediments of Sicily is slightly younger.

Distribution: Except for the type locality, *H. keuperina* was found at 28 other localities (see Tab. 1). These localities can be grouped together into four geographic units:

– Weserbergland: upper section of the "Isenberg-Horizont" (= Lower Lehrbergbank, DUCHROW 1984: 299) at the Köterberg SE Rischenau (for profile see SANDER 1977: pl. 2), and near Polle NNW Holzminden.
– Haßberge: upper part of the Lower Lehrbergbank near Leinach and near Junkersdorf.
– Keuperbergland of Baden-Württemberg: upper part of the Lower Lehrbergbank in the Löwensteiner Berge, Mainhardter Wald, Remstal, Schurwald.
– Frankenhöhe: upper part of the Lower Lehrbergbank in the Ansbach area (Strüth, Götteldorf, Adelmannsdorf).

There is little doubt that *H. keuperina* could be discovered at some more outcrops by searching directly for it. The species is at present unknown from the lower part of the Lower Lehrbergbank, the Middle and Upper Lehrbergbank and also from the lacustrine Ochsenbachschicht (Norian, Stubensandstein-Schichten; see BRENNER 1973) in the Stromberg Keuper (NW-Baden-Württemberg).

Carbonate microfacies and associated fauna: The petrography, palaeontology and palaeoecology of the Lehrbergschichten are described in detail by SEEGIS (1996) and are therefore only summarized here. At the type local-
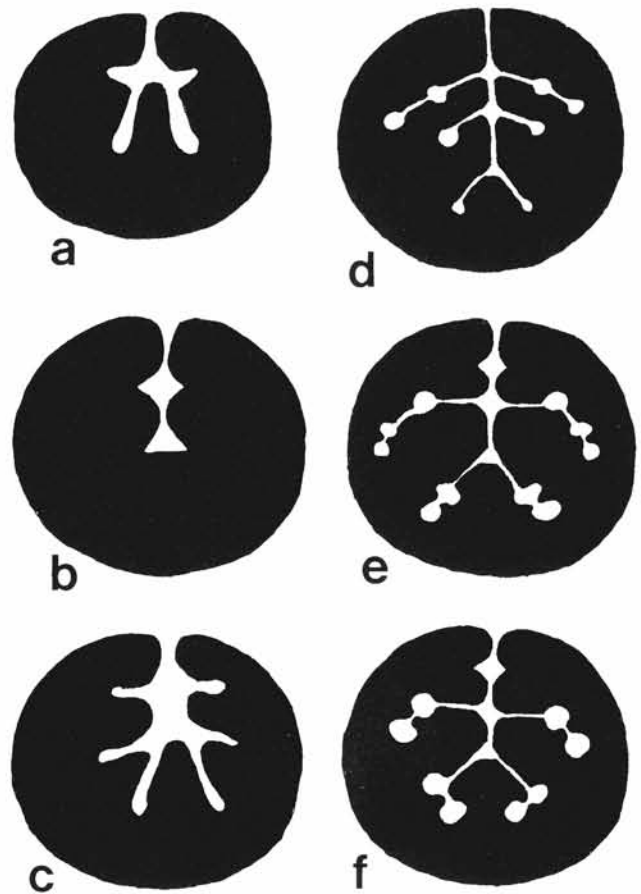

Fig. 6. Idealized cross sections of different species of *Helicerina*. – **a:** *Helicerina spinosa* BRÖNNIMANN & MASSE (= type species); **b:** *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO; **c:** *Helicerina keuperina* SEEGIS n. sp.; **d:** *Helicerina kalankyra* (EBLI); **e:** *Helicerina kainachensis* FENNINGER & HUBMANN; **f:** *Helicerina ruttei* SCHWEIGERT n. sp. – Not to scale.
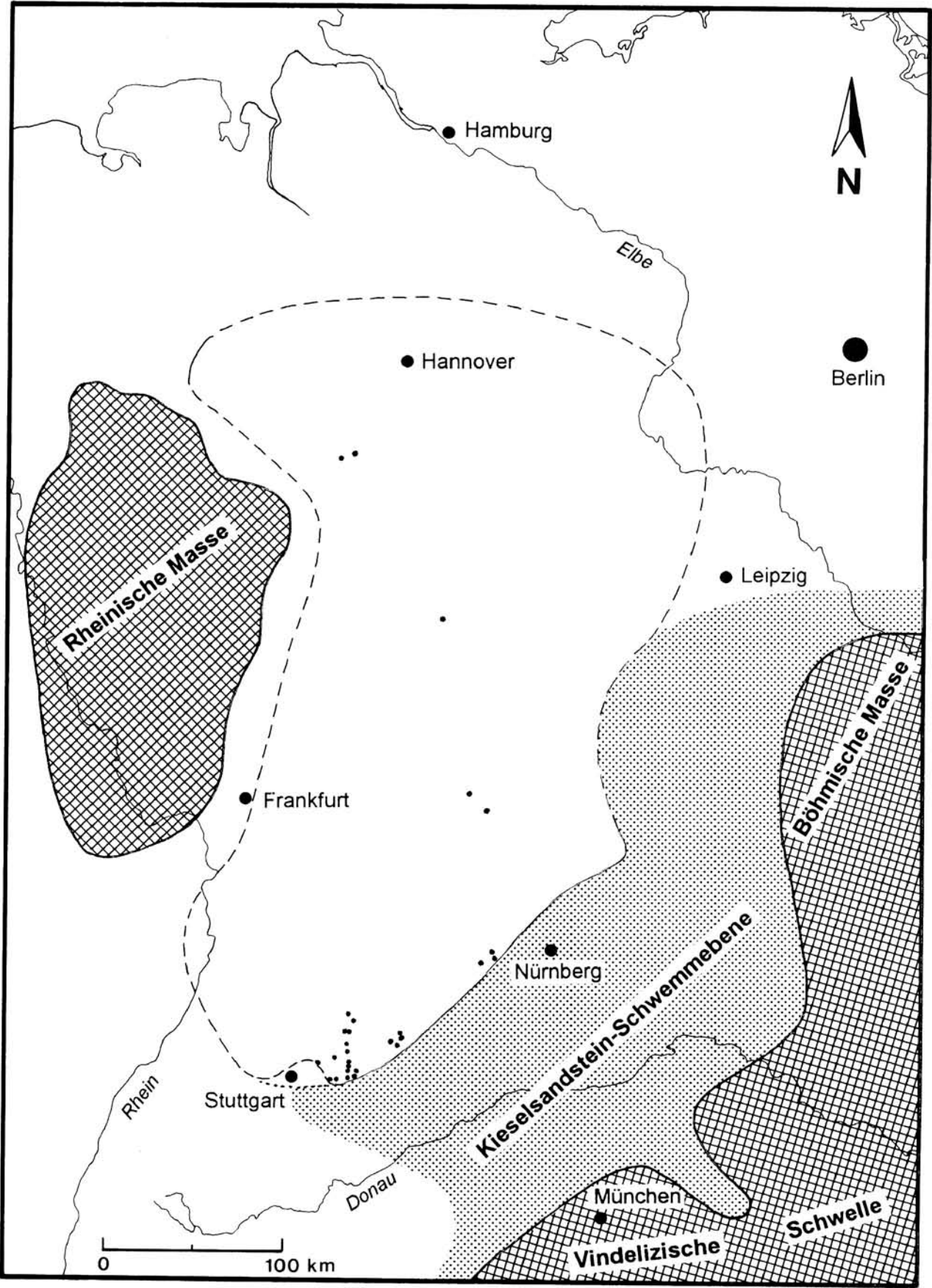
Fig. 7. Late Carnian palaeogeography of the German Basin, maximum extension of the Lehrberg lakes and geographic distribution of *Helicerina keuperina* SEEGIS n. sp.

ity. *H. keuperina* is found in a dolomitic packstone consisting of molluscan and ostracod shells and fine, detrital quartz sand. Usually, the coprolites occur in clusters. Some thin, winnowed layers consist almost exclusively of crustacean coprolites. The associated fauna has a very poor species richness. It comprises gastropods (*Triasamnicola* sp., "*Promathildia*" *theodorii* [BERGER]), pelecypods (*Pseudocorbula keuperina* [QUENSTEDT]), indeterminable ostracods and isolated fish remains (*Lepidotes* sp.). Although only weathered fragments of bedrock have been found at this locality, the dolomitic layer can be correlated with the upper part of the Lower Lehrbergbank by the occurrence of *Pseudocorbula keuperina*, a species which within the Lehrberg Beds is restricted to this horizon.

In the Isenberg horizon of the Weserbergland, *H. keuperina* is, to the present knowledge, restricted to a laminated, dolomitic mudstone devoid of any other fossils.

In the Lower Lehrbergbank of Baden-Württemberg, the same species is found especially in mud- to wackestones with quartz sand and a few molluscs and ostracods. As at the type locality, it often occurs in clusters. In Baden-Württemberg, *H. keuperina* is missing or not preserved in grain- and packstones consisting of molluscan shells (partly with micrite envelopes), whereas in Franconia, *H. keuperina* is found in such facies. The associated fauna in both areas comprises ostracods, gastropods ("*Promathildia*" *theodorii* [BERGER], *Triasamnicola* sp.), pelecypods (*Pseudocorbula keuperina* [QUENSTEDT], *Unio keuperinus* BERGER), ostracods (*Limnocythere* cf. *keuperea* WILL, *Simeonella brotzenorum alpina* KOZUR, *Darwinula* sp., and an undetermined, smooth-shelled cypridacean ostracod) and isolated fish remains (*Lepidotes* sp., *Turseodus* sp., *Semionotus* sp., dipnoans, actinistians).

P a l a e o e c o l o g y : The Lehrbergbänke were deposited in very shallow, hydrologically closed lakes which became more saline towards their center, depending on the high evaporation rate in a warm, dry climate (BRENNER 1973;

Tab. 1. Records of *Helicerina keuperina* SEEGIS n. sp. in Germany.

Topographic map 1:25000	Locality	Gauß-Krüger-Coordinates
4022 Ottenstein	NNE Polle	35 28 080 / 57 52 480
4121 Schieder-Schwalenberg	S Köterberg	35 22 170 / 57 46 940
4927 Creuzburg	Lengröden	35 88 380 / 56 55 560
5728 Oberlauringen	Leinacher Steige	36 00 060 / 55 66 350
5829 Hofheim i.UFr.	ESE Junkersdorf	43 98 410 / 55 52 400
6529 Markt Erlbach	Götteldorf	44 00 450 / 54 75 200
6629 Ansbach/Nord	ENE Adelmannsdorf	44 02 140 / 54 73 240
6629 Ansbach/Nord	S Strüth	43 94 600 / 54 66 680
6823 Pfedelbach	E Storchsnest, „Schleifsteinklinge"	35 42 580 / 54 42 160
6923 Sulzbach a.d.Murr	ESE Zwerenberg, Harbach	35 40 540 / 54 30 470
6923 Sulzbach a.d.Murr	NE Kieselhof	35 42 020 / 54 30 360
6923 Sulzbach a.d.Murr	ENE Bubenorbis	35 46 220 / 54 39 060
6924 Gaildorf	SE Eutendorf, Bilmersbach	35 58 260 / 54 32 320
6925 Obersontheim	W Hinteruhlberg, Mailandbach	35 70 160 / 54 35 760
6925 Obersontheim	NNW Hettensberg, SE „Geigersberg"	35 69 890 / 54 34 960
7023 Murrhardt	WNW Lutzenberg, „Teufelshalde"	35 39 380 / 54 20 380
7023 Murrhardt	W Siebenknie, Eschelbach	35 38 140 / 54 26 950
7025 Sulzbach-Laufen	SE Immersberg, „Kohlklinge"	35 65 260 / 54 27 080
7122 Winnenden	N Winterbach, „Burgklinge"	35 35 470 / 54 09 140
7122 Winnenden	NE Korb, W „Trombach"	35 27 330 / 54 13 080
7122 Winnenden	NE Öschelbronn, N „Körnerrain"	35 34 480 / 54 17 400
7123 Schorndorf	W Buhlbronn, Bodenbach	35 37 460 / 54 12 100
7123 Schorndorf	NNE Schornbach	35 38 100 / 54 11 470
7123 Schorndorf	SW Schornbach	35 37 030 / 54 09 610
7123 Schorndorf	NE Plüdershausen, S „Lochtobel"	35 45 000 / 54 07 540
7222 Plochingen	S Winterbach, Lehnenbach	35 35 430 / 54 04 710
7222 Plochingen	SW Schnait	35 29 630 / 54 05 200
7222 Plochingen	ENE Schnait, „Pfaffenholz"	35 31 550 / 54 06 660
7223 Göppingen	ESE Schorndorf, „Galgenberg"	35 40 480 / 54 06 700
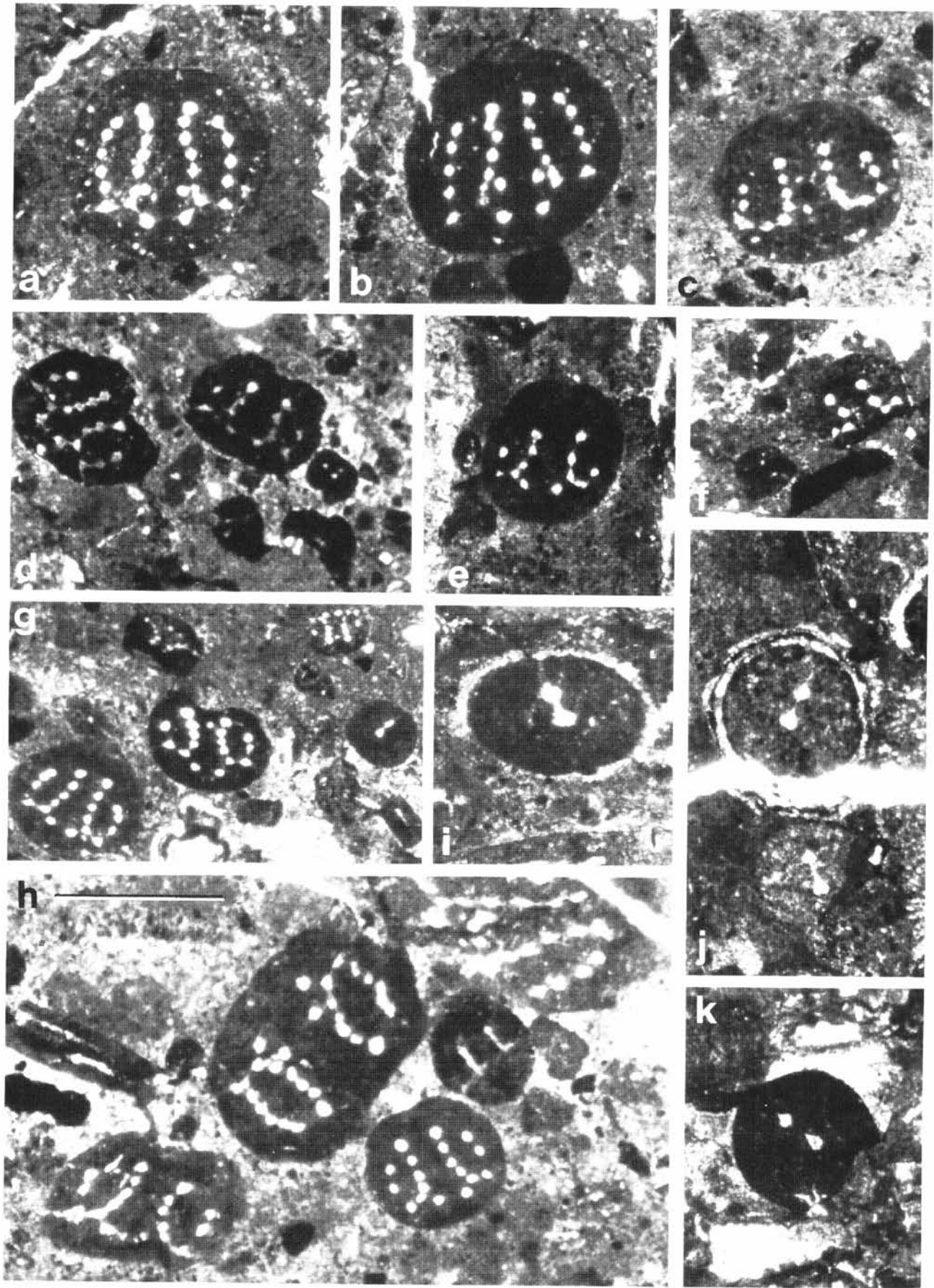
SEEGIS 1992, 1996). The low-diversity, mainly limnic fauna with a few brackish forms (*Pseudocorbula, Simeonella*) points to a restricted environment. Hence, the producer of *H. keuperina* lived in the lacustrine realm. Body remains of this animal are at present unknown. It is supposed that the calcified chitinous skeletons of this decapod crustacean were in most cases destroyed by scavengers before they could be buried. Such body remains might at best be expected in the central part of the lake (i.e., in the Leine valley and the Weserbergland), where there was less disturbance of the lake-bottom sediments by waves and subaerial exposition during climatically drier periods.

Microcoprolites from ferruginous limestones of the Subbetic Jurassic of Southern Spain (A. FELS)

Within the pelagic Jurassic of the External Subbetic of Southern Spain, red limestones besides brown ferruginous and ferromanganese crusts and nodules reflect reduced and condensed sedimentation, respectively. A special type of condensed sediment occurs in a Middle Jurassic section from the Sierra del Reclot (Province of Alicante). A yellow limestone yields microcoprolites as the only bioclasts. They are partly densely packed, and the primary carbonate is strongly replaced by goethite and hematite. The condensed section is regionally dated by ammonites indicating Early Bajocian Sauzei Zone (SEYFRIED 1978; FELS 1995). However, within the studied condensed section, which is about 30 cm thick, no ammonites have been found. The yellow limestone is slightly stained by goethite. Brown goethite streaks of diagenetic origin are abundant.

The carbonate micrite and microcoprolites were deposited through intervals of reduced carbonate sedimentation within the condensed section. As the substrate was intensely colonized by crabs and other benthic crustaceans, microcoprolites accumulated. They are not equally distributed within the micrite but occur densely packed in lenses. Although many of them are deformed by compaction and thus not determinable, others are well preserved, the better the closer they are positioned to a goethite crust. During repeated interruptions of sedimentation, the carbonate mud lithified and hardgrounds

developed, with ferruginous, stromatolite-like crusts growing upon them. The carbonate staining is supposed to be synsedimentary as it is evenly distributed throughout the limestone. The coprolite matter was replaced after lithification due to the different grade of ferruginous density relative to the proximality of a goethite crust. Two different types of microcoprolites could be identified within this section (for description see below).

Crustacean microcoprolites of Middle Jurassic age have not yet been described from Spain. Only few coprolite species have been reported from other localities of the Middle Jurassic.

Favreinidae VIALOV 1978

Favreina belandoi n. sp.
Figs. 8a-h, 10a-b

Derivatio nominis: in honour of J. BELANDO from La Romana for his hospitality during field work.
Holotype: the specimen on Fig. 8a, from a thin section housed at the Museum of Natural History Stuttgart (SMNS 62628).
Paratypes: specimens in Fig. 8b-h, same thin section as the holotype.
Locus typicus: Sierra del Reclot, section R VIII L NW Algayat; for location see FELS 1995: Fig. 45.
Stratum typicum: ferruginous limestones of Bajocian age.

Diagnosis: species of the genus *Favreina* with two or four separate canals arranged in the ventral part of the coprolite and two rows of additional canals on both symmetric parts.

Description: *Favreina belandoi* n. sp. cannot be characterized by its total number of internal canals. It must be defined by the shape and arrangement pattern of canals which is correlated with the diameter of the microcoprolites. *Favreina belandoi* differs from all other species of *Favreina* by the presence of a pair of isolated canals in the "ventral" part of most growth stages of the microcoprolites, except of the smallest ones. In larger specimens a second pair of canals develops in the dorsal direction of the earlier formed canals, thus in cross section describing a trapezoid. The other canals are arranged in two symmetric pairs of rows. The inner rows run more or less parallel to each other, whereas the outer ones, seven at least, are slightly curved towards the "dorsal" groove. In every growth stage, new canals only developed at the "dorsal" part of the coprolite (see Fig. 9).

In cross sections the canals of one row are clearly linked by faint "lines", but all rows are clearly separated from each other. These "interconnecting lines" are also visible in ferruginous specimens edged from the sediment (Fig. 10a-b). *Favreina belandoi* n. sp. has a subcircular to oval cross section, particularly within the larger specimens. In general, *Favreina belandoi* n. sp. is larger than the co-occurring *Helicerina siciliana*, but its mean diameter of about 420 µm is nearly identical.

Two rows of canals on each half of the coprolite are also present in a single still unnamed specimen from the

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← Fig. 8. Crustacean microcoprolites from the Subbetic Middle Jurassic of Southern Spain.
a-g: *Favreina belandoi* FELS n. sp., Bajocian, Sierra del Reclot (Prov. Alicante), thin section no. VIII L 5h (SMNS 62628). –
a: holotype; b-f: additional specimens demonstrating the increasing number of canals in specimens of increasing diameters; g: *Favreina belandoi* FELS n. sp., together with *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO.
h-k: *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO. – h: thin section no. VIII L5a (SMNS 62629); i: thin section no. VIII L 5d (SMNS 62630); k: thin section no. VIII L 5e (SMNS 62631). – Scale bar: a-f, h-k = 0.5 mm; g = 0.25 mm.
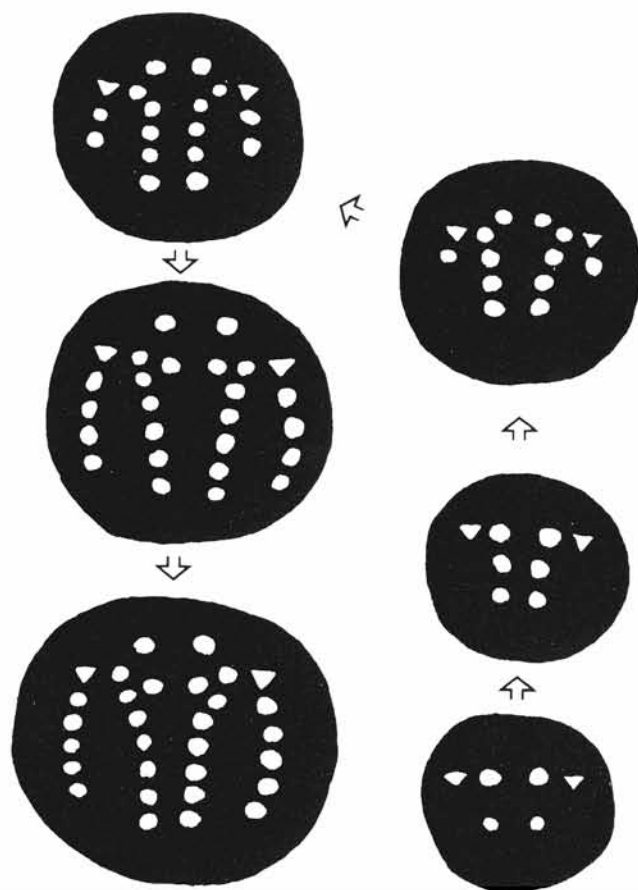
Fig. 9. Ontogenetic development of *Favreina belandoi* FELS n. sp. Number of canals increase with diameter. – Not to scale.

Fig. 10. a-b: *Favreina belandoi* FELS n. sp., two specimens of different diameters and number of canals; **c:** *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO. – Shape of the internal canal system of hematitic specimens detached with acid from the rock (SEM photographs). – Middle Jurassic, Bajocian, Sierra del Reclot (Prov. Alicante).

Anisian of the Southern Alps (SENOWBARI-DARYAN et al. 1993) and in *Favreina prima* from the Devonian of Morocco (HERBIG 1993). It seems that some species of *Parafavreina* are closer to *Favreina belandoi* than to other ichnospecies attributed to *Favreina* so far. This view is favoured by the occurrence of triangular sections of canals apart from rounded ones in *F. belandoi* . Perhaps in the future a revision of both genera will be necessary, in which the arrangement of canals should have a higher diagnostic value than the shape of the canals.

Helicerina siciliana SENOWBARI-DARYAN,
SCHÄFER & CATALANO 1979
Figs. 8g, i-k, 10c

1979 *Helicerina siciliana* n. sp. – SENOWBARI-DARYAN et al.: 316, pl. 1, figs. 1-9.
1986 *Helicerina siciliana* SENOWBARI-DARYAN, SCHÄFER & CATALANO, 1979 – MOLINARI PAGANELLI et al.: 314, fig. 4c; pl. 1, fig. 3.

Description: see SENOWBARI-DARYAN et al. 1979.

Occurrence: Late Triassic of Sicily (SENOWBARI-DARYAN et al. 1979), Bajocian of Spain (this paper).

There is no difference in morphology at all between the type material from the Triassic and the much younger specimens from Spain. Compared with more differenti-
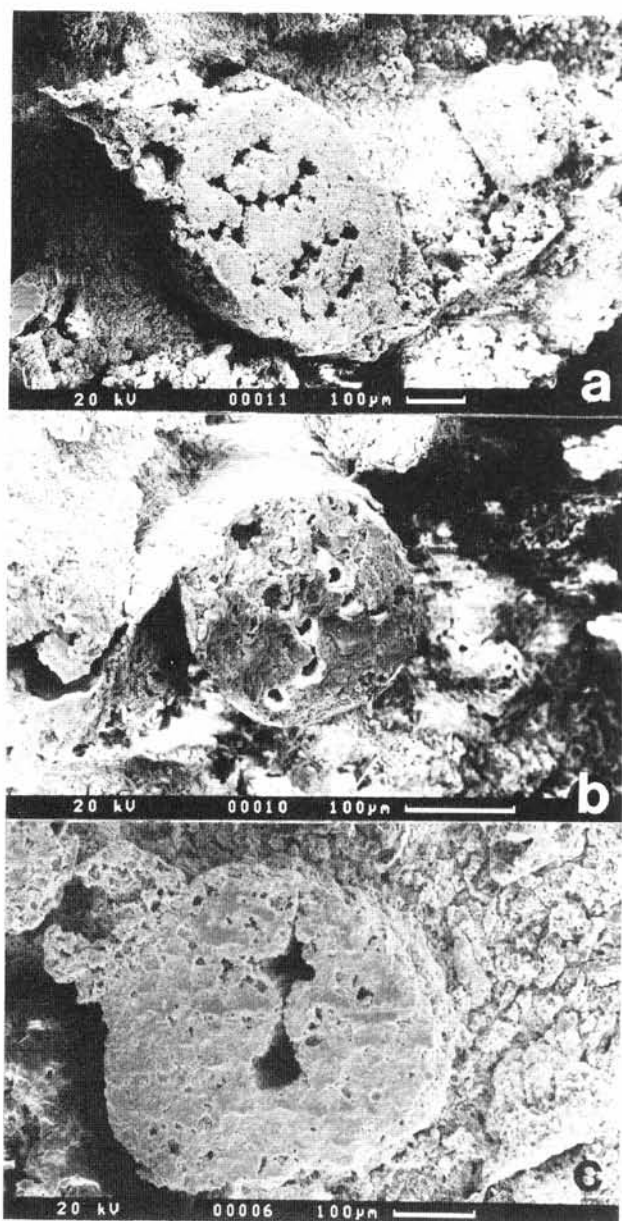
ated species of *Helicerina* (*H. ruttei, H. kainachensis*), *H. siciliana* exhibits the central canal system with a diamond-shaped dorsal canal and a triangular ventral one. *Helicerina siciliana* is preserved with well-crystallized hematite making it possible to etch them out of the limestones (Fig. 10).

As suggested by thin section images the different shape of the canals can be well observed by SEM investigations. The mean diameter of the coprolites is about 417 μm.

Many but not all specimens of *Helicerina siciliana* are

surrounded by a sparitic corona. The same observation can be achieved in many other crustacean microcoprolites (pers. comm. Dr. J. BLAU, Genève), and within our material in some of the specimens of *Helicerina ruttei*. This corona may represent sparitic cements which were precipitated in subcircular moulds around the microcoprolites after an early diagenetic shrinkage.

Palaxius salataensis BRÖNNIMANN, CROS & ZANINETTI 1972
Fig. 11 a-b

1972 *Palaxius salataensis* n. sp. – BRÖNNIMANN, CROS & ZANINETTI: 923, pl. 1, figs. 1-10, 12; text-fig. 2a-f.
1984 *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI 1972 – MOLINARI PAGANELLI: 324, pl. 2, fig. 6; text-fig. 11.
cf. 1992 *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI 1972 – SENOWBARI-DARYAN et al.: 192, fig. 3k, o-r.
1993 *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI 1972 – BLAU et al.: 208, fig. 9 J-M.
1996 *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI 1972 – MASSE & VACHARD: figs. 2-3.

Synonyms: see BLAU et al. 1993.

Occurrence: Late Carboniferous, Permian, Late Triassic, Early Jurassic (this paper), Late Cretaceous.

This coprolite species has never been reported from Spain before. Moreover, it is the first true occurrence from the Jurassic. The type material is derived from "infraliassic" limestones of the Dolomites, which are, according to BRÖNNIMANN et al. (1972), most probably Rhetian in age. However, a liassic age seems to be more likely for these limestones (Dr. J. BLAU, pers. comm.).

P. salataensis occurs in micritic limestones of Late Liassic age in the Sierra del Reclot (FELS 1995: fig. 58). According to ammonite findings in the same area a Toarcian age of the condensed layer could be determined. The specimens are only poorly preserved, but their specific attribution to *P. salataensis* is beyond doubt. The microcoprolites are associated with small foraminifers, filaments, echinoid spines, and masses of radiolarians. It seems that the microcoprolites are concentrated in some particular parts within the bioturbated rock. This possibly indicates that the producers of these microcoprolites were endobenthic.

Other species which also possess four internal canals in cross sections are *Palaxius tetraochetarius* PALIK 1965, *P. darjaensis* SENOWBARI-DARYAN & SILANTIEV 1991, *P. montemeranoensis* BLAU & GRÜN 1989, and the recently described *P. caucaensis* BLAU, MORENO & SENFF 1995. They all differ from each other in their arrangement of canals, as it was shown by SENOWBARI-DARYAN & SILANTIEV (1991) and BLAU et al. (1995). Nevertheless it is possible, that specimens of *Palaxius salataensis* from the Carboniferous, from the Permian or from the Triassic are only hardly distinguishable from younger representatives of other similar species because of their sometimes
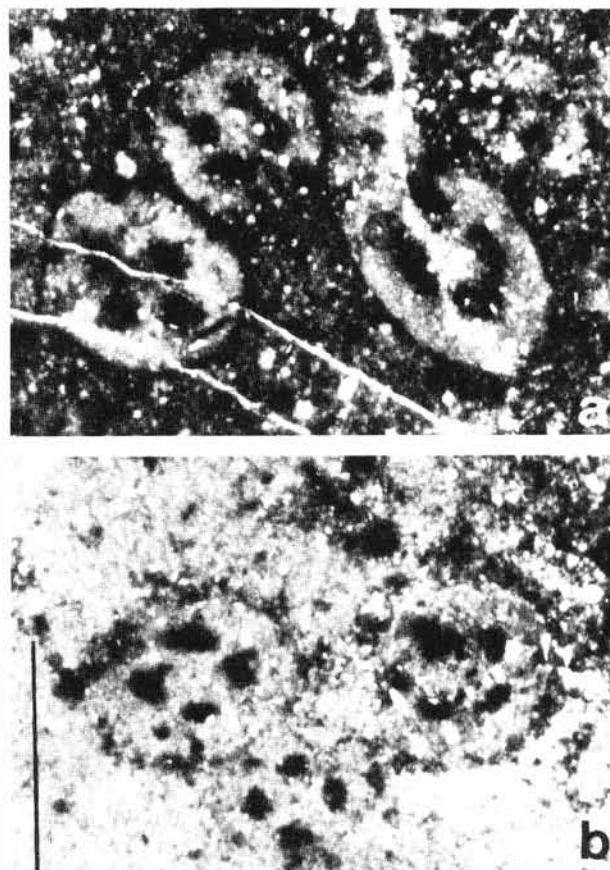

Fig. 11. a-b: *Palaxius salataensis* BRÖNNIMANN, CROS & ZANINETTI, thin section no. VIII a4 (SMNS 62624). Early Jurassic, Toarcian, Sierra del Reclot (Prov. Alicante). – Scale bar: a-b = 0.5 mm.

poor preservation and their lack in additional characteristic morphological features. SENOWBARI-DARYAN & GRÖTSCH (1992) reported an increase in size from the Palaeozoic to the Cretaceous. This was critisized by BLAU et al. (1993) who argued that the size may vary due to different ontogenetic stages, and the material studied by SENOWBARI-DARYAN & GRÖTSCH (1992) does not allow such statistics. The arrangement of canals seems to be slightly different in the Palaeozoic specimens reported by SENOWBARI-DARYAN et al. (1992) in the relation between the canal size and the diameter of the coprolites.

Microcoprolites from the Upper Jurassic Ota Limestone of Portugal (R.R. LEINFELDER)

Up to date, *Favreina guinchoensis* BRÖNNIMANN 1976, was the only known crustacean microcoprolite species from the Jurassic of Portugal. It was originally described by RAMALHO (1971) from the Sintra area as "*Favreina* cf. *salevensis*". Other microcoprolites of the *Favreina* type were mentioned from the base of the Valanginian of the same area.

The reefal to lagoonal Ota Limestone was investigated in detail by LEINFELDER (1992, 1994). In a comprehensive description of synsedimentary karstic fissures within the

reef limestones, a microcoprolite bearing facies type was mentioned occurring as a sedimentary infill of some of the fissures. Within this facies type, internally structured crustacean microcoprolites are the predominating particles forming cross laminated layers This coprolite subfacies is embedded in another bioclastic facies type which yielded calcareous algal-type microproblematica and cyanobacteria (*Bacinella irregularis* RADOIČIĆ, "*Cayeuxia*" sp.), foraminifers (e.g. *Everticyclammina virguliana* [KOECHLIN], *Lithocodium aggregatum* ELLIOTT, associated with *Troglotella incrustans* WERNLI & FOOKES, see SCHMID & LEINFELDER 1996), echinoid spines, serpulids, intraclasts, bivalve shell fragments, and oncoids, thus indicating moderately high energy conditions in an assumed low water depth. Besides these particles, crustacean microcoprolites occur very rarely. They are of another form genus as those which are abundant in the cross-bedded layers. Probably, both forms represent different palaeoecological environments. The large amounts of microcoprolites within the cross bedded cave fill facies suggests that their producers lived within the open carstic fissures when they were flooded after a rapid sea level rise. It cannot be proven but seems possible that they are remnants of a mixed salinity, intertidal coastal rocky environment. The other coprolite type is derived from decapods living in a lagoonal shallow water environment together with the other fauna and flora. These organisms occasionally washed into fissures which were still partially open. A late Kimmeridgian age both of the upper part of the Ota Limestones and of the karstic fissure fillings is indicated by the co-occurrence of diagnostic dasyclad algae such as *Clypeina jurassica* and *Campbelliella striata*, together with the foraminifer *Alveosepta jaccardi* (LEINFELDER et al. 1988).

Favreinidae VIALOV 1978

Petalina n. gen.

Derivatio nominis: The arrangement of the canals looks like the petals of a flower.

Type species: *P. hexalunulata* n. sp.

Diagnosis: The new coprolite genus *Petalina* is characterized by a bilaterally symmetrical rim of canals which have half-spherical cross sections. Canals within the symmetry plane are absent.

Petalina hexalunulata n. sp.
Fig. 12 a-c

Derivatio nominis: according to the six hemispherical canals visible in cross sections.
Holotype: the specimen illustrated on Fig. 11a; acetate peel housed at the Museum of Natural History Stuttgart (SMNS 62632/1).
Additional material: Four specimens in thin section SMNS 62632/2 from the same rock sample as the acetate peel with the holotype specimen.
Locus typicus: Alenquer section, Lusitanian Basin, Portugal.

Stratum typicum: synsedimentary karstic fissures of the Ota Limestone, subsequently flooded and infilled by marine lagoonal sediments (Late Jurassic, Kimmeridgian).

Diagnosis: Microcoprolites of the new genus *Petalina* with three bilaterally symmetric internal canals.

Description: The few coprolite specimens have an average diameter of about 570 mm. Because of the lack of any morphological features on the surfaces of these microcoprolites a ventral-dorsal orientation is difficult. The rim of canals is not arranged in the center of the coprolite, and probably it approaches to the "dorsal" region, at it is also the case both in *Lercarina* (see SENOWBARI-DARYAN 1988) and in *Helicerina*.

The arrangement and shape of the canals is clearly different from *Favreina hexaochetarius* PALIK 1965, *F. martellensis* BRÖNNIMANN & ZANINETTI 1972 and *F. radiata* SENOWBARI-DARYAN & KUSS 1992, all of them also exhibiting six internal canals. The form genus *Agantaxia* KRISTAN-TOLLMANN shows strong morphological affinities to *F. hexaochetarius*. The shape of canals in *Agantaxia* is caused by the merging of a pair of individual canals by interconnecting lines. Hence we agree with SENOWBARI-DARYAN & KUSS (1992: 132) that *Agantaxia* could be well included in *Palaxius*.

Several other crustacean microcoprolites exist which also comprise 6 internal canals. Most of them have rounded cross sections, and some species may be separated from each other on the base of their arrangement of canals, as it was discussed by SENOWBARI-DARYAN & KUSS (1992). For example, the species *Favreina radiata* was considered to be different from *F. hexaochetarius* PALIK and *F. martellensis* BRÖNNIMANN & ZANINETTI due to its radial symmetry instead of a clear bilateral symmetry of the latters. However, all microcoprolites are expected to have a more or less bilateral symmetry in analogy of the bilateral symmetry of the coprolite producing animal's anatomy (Dr. J. BLAU, pers. comm.).

Petalina hexalunulata n. sp. is restricted to the bioclastic microfacies type generally superimposing the cross-bedded cave fill with *Favreina* type microcoprolites described by LEINFELDER (1994: 87). This *Favreina* facies is completely devoid of *Petalina hexalunulata*, although there is only a distance of few millimeters between both occurrences in the same rock sample.

Favreina prusensis (PARÉJAS 1948)
Fig. 12 d-e

* 1948 *Coprolithus prusensis* – PARÉJAS: 516, figs. 36, 41-42.
  1969 *Favreina prusensis* (PARÉJAS) – CUVILLIER et al.: 184, pl.1, figs. 12-13.
  1984 *Favreina prusensis* (PARÉJAS, 1948) – MOLINARI PAGANELLI et al.: 441; fig. 14.
  1985 *Favreina prusensis* (PARÉJAS) – BENEST: pl. 6, fig. 9.

Synonyms: see MOLINARI PAGANELLI et al. 1984. Lectotype designated by BRÖNNIMANN 1977.

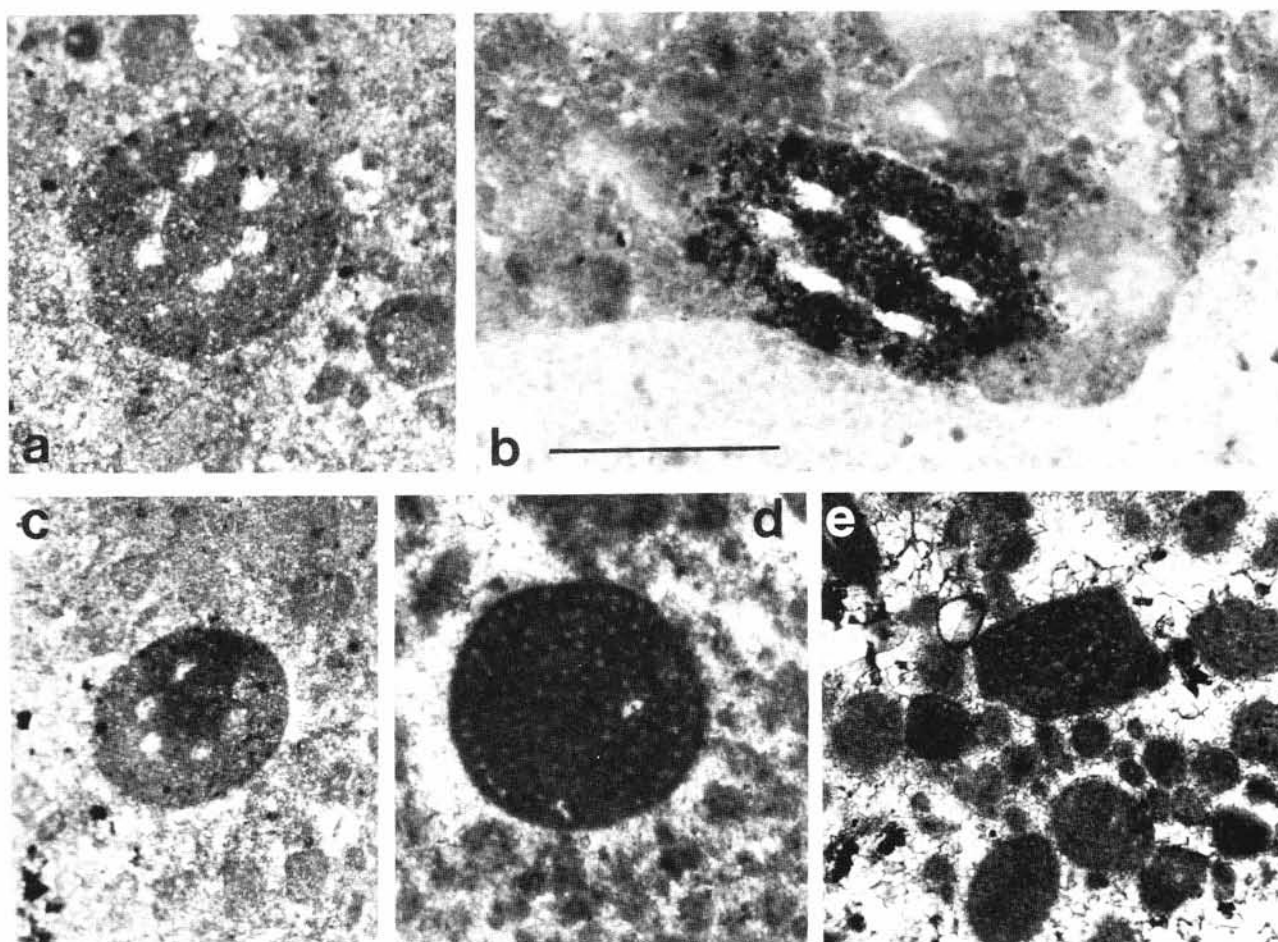Occurrence: Late Jurassic, Kimmeridgian/Tithonian.

Fig. 12. Crustacean microcoprolites from the Kimmeridgian Ota Limestone of Portugal.
a-c: *Petalina hexalunulata* LEINFELDER n. gen. n. sp.: **a:** holotype, acetate peel SMNS 62632/1: **b:** additional specimen from thin section no. SMNS 62632/2a of the same sample; **c:** additional specimen from acetate peel SMNS 62632/1.
d-e: *Favreina prusensis* (PARÉJAS), thin section no. SMNS 62632/2b. **d:** large specimen; **e:** facies type with numerous pellets. –
Scale bar: a-b = 0.5 mm; c = 1mm; d-e = 0.375 mm.

Favreina prusensis was originally described from the Late Jurassic of Turkey. It is hardly possible to count the exact number of internal canals which is surely variable according to our experiences with other coprolite species, and there are often some small sparitic particles within the coprolite which pretend additional canals. One of the best preserved specimens of *F. prusensis* from a possibly intertidal marine infill of a karstic fissure of the Alenquer section (Portugal, see above) comprises between 150 and 160 canals. SENOWBARI-DARYAN & KUSS (1992) assumed a range between 66 and 136 canals for that species, so that the new specimens exhibit the largest number of canals ever known from that ichnospecies. The diameters of *Favreina prusensis* vary between 540 and 1260 μm (SENOWBARI-DARYAN & KUSS 1992). The new specimens from Portugal reach 570 μm. Hence it is astonishing why the specimens from Portugal despite exhibiting the highest number of canals are not the ones with the largest size. Either the diameters are variable due to different diagenetic conditions, e.g. an early stage of shrinkage during pellet formation, or the form species *Favreina prusensis* was produced by a different, but very close anomuran spe-

cies. Probably both factors will make it impossible to recognize microcoprolites on the biospecies level. Large numbers of canals are also known from the very large coprolite species *Favreina multicanalis* FÖRSTER & VON HILLEBRANDT 1984, but the published material of this species from the Kimmeridgian of Chile is very poorly preserved, so that its value for a comparison with other species seems to be very restricted. Somewhat similar to *Favreina prusensis* is *Parafavreina huaricolcanensis* described from the Late Triassic of Peru (SENOWBARIDARYAN & STANLEY 1986). This species was attributed to *Parafavreina* because of the sometimes visible triangular cross sections of the canals. It is in our opinion more likely that the triangular shape of only few of these canals exhibiting a very small diameter is nothing else than the typical cross section of isolated calcite spar crystals.

Interestingly another new species of *Favreina* which was preliminary figured by HERRMANN (in LEINFELDER et al. 1994: pl. 4, fig. 5) from the Oxfordian of Romania occurs in a quite comparable environment like *F. prusensis*. The arrangement of canals within the new Romanian species is very close to that of *Favreina prusensis* and may

indicate that the producers of both taxa are related to each other to a high degree, probably both in their systematic position and in their palaeoecological requirements.

General aspects – discussion

Although our examples of fossil crustacean microcoprolites are heterogeneous in age, systematic position, environmental and palaeogeographic occurrence, their comparative analysis allows to deduce general aspects. These include taxonomic problems, the frequently discussed question of practicability of crustacean microcoprolites for age determinations, and palaeoecological as well as evolutionary implications.

Ontogenetic variability in fossil microcoprolites

Most authors describing fossil crustacean microcoprolites presume that within a range of diameters the number of canals in transversal sections should be constant. Only in some species of *Favreina* (see SENOWBARI-DARYAN & KUSS 1992) the number of canals was shown to vary with their size. When proposing a lectotype of *Favreina salevensis* (PARÉJAS), already BRÖNNIMANN (1976) stated that the smallest specimens exhibit a lower number of canals than the larger ones. He assumed that the smaller specimens derive from juvenile individuals. Later, BRÖNNIMANN, CARON & ZANINETTI (1972) found, that within their newly described coprolite species *Parafavreina thoronetensis* the specimens differ in the number of canals, a fact which was recognized as being correlated with different ontogenetic stages of a single decapod species. Despite of these observations other crustacean coprolite species have been described which were said to have a very large but constant number of internal canals. Mostly these species are based on only one single specimen (e.g. *Favreina guinchoensis* BRÖNNIMANN 1976), or the type series consists of very poorly preserved material, so that the number of canals can hardly be estimated (e.g. *Favreina multicanalis* FÖRSTER & VON HILLEBRANDT). Another problem may be the occurrence of abnormal microcoprolites. As our example within the species *Helicerina ruttei* shows, the shape and arrangement of canals may become very simplified (see Fig. 2h), and then it somewhat resembles the genus *Palaxius*. An isolated specimen of such morphology would be certainly described as an individual species. Hence it seems quite possible that other species whith a very simple internal structure are not related to a valid crustacean biospecies but may represent only microcoprolites from sick individuals normally producing other internal structures within their microcoprolites. For example, the very simple-shaped *Palaxius groesseri* BLAU, GRÜN & SENFF 1993 from the Late Triassic of Colombia may have been produced by a separate valid biospecies, but it is also possible, that it only represents an irregular form of *Palaxius colombiensis* which was published in the same paper from the same locality and stratum.

Diversity of microcoprolites versus diversity of their producers

When fossil crustacean microcoprolites were identified and described for the first time, a very simple diagnosis was given for one of the oldest crustacean coprolite genus "*Favreina*". Since that time a large number of species had been described, although there are only very few characteristic features in microcoprolites which may be useful for taxonomic subdivision:
– size and shape of the coprolite in cross section;
– number, shape and arrangement of the internal canals.
Investigations of modern faecal pellets and also fossil microcoprolites, however, do not necessarily exhibit only a single type of internal canals. For example, *Parafavreina thoronetensis*, which has much in common with our newly described species *Favreina belandoi*, exhibits a *Palaxius*-like canal in the ventral part of the coprolite (see BLAU et al. 1994). In the same part of the coprolite, a triangular canal is developed in *Favreina belandoi*, which otherwise only yields rounded shaped canals which is why we attributed this species to *Favreina* and not to *Parafavreina*.

Because of their common occurrence in many shallow water carbonates, crustacean microcoprolites are said to be useful for stratigraphic purpose (SENOWBARI-DARYAN & KUSS 1992; BLAU et al. 1993). Some species seem to have had a short stratigraphic range whereas others span over several stages or even systems. Interestingly, coprolite species with a simple internal canal system have larger stratigraphic ranges than others which exhibit more complicated canal patterns. If the internal structures are very simple it seems difficult or even impossible to distinguish between different species, as it is discussed above at the example of *Palaxius salataensis*. We believe that the evolution of the gross morphology of the decapods is much more diverse and rapid than that of the digestive tract, which is rather conservative.

When looking at the number of crustacean species that lived in the same time interval as a coprolite ichnospecies did, it becomes obvious that it is completely impossible that all coprolite producing crustacean species can be recognized or subdivided by their faecal production. Because complete crustacean specimens are only rarely fossilized, we only know a small percentage of co-occurring species. Compared with modern species of freshwater crabs, a very large number of species have been described which can be separated mainly, and sometimes only, by micromorphological features, e.g. by their gonopods. Surprisingly, it is hardly possible to distinguish the oldest known fossil freshwater crab *Proballaya quenstedti* (ZITTEL) from the modern freshwater crab *Stoliczia goal* NG (1993) from southeastern Asia only by means of the morphology of the carapax. It is quite obvious that the number of possible features in coprolite morphology never reaches the number of crustacean species even if we assume that a lot of coprolite species are not described yet or will remain unknown forever due to preservational bias.

From our point of view we believe that crustacean

microcoprolites only allow to distinguish different families of producing crustaceans, but a separation on the biospecies level seems rather impossible. Therefore, only microcoprolites which exhibit a more complicated or somewhat characteristic arrangement of canals are in fact useful for stratigraphic purposes.

Palaeoecological implications

Up to the present,there are only two known examples of fossil crustacean microcoprolites coming from nonmarine environments: *Helicerina ruttei* n. sp. and *Helicerina keuperina* n. sp., both described above. *H. keuperina* gives evidence that even at the beginning of crabs, they were just adapted to settle in nonmarine environments. The earliest known true crabs (*Eocarcinus praecursor* WITHERS) occur in the Early Jurassic. It is generally accepted that the brachyuran decapods derived from pemphicid ancestors in the Late Triassic (GLAESSNER 1928, 1960; FÖRSTER 1967, 1979, 1986; VIA & SEQUEIROS 1993). Interestingly, the form genus *Helicerina* also occurs in the Norian Hauptdolomite Formation. Recently, ZANKL & MERZ (1994) discussed the influence of freshwater during the precipitation of the carbonate, which is considered to have formed in a very shallow intertidal environment marked by loferite cycles. From that point of view this would not have been a favourable environment for nectonic shrimp-like anomuran decapods, but a paradise for benthic crab-like arthropods.

On the other hand decapods producing microcoprolites of the *Helicerina* type also occur in deep marine environments like in our example from the Bajocian of Southern Spain. It is quite obvious that both records of *Helicerina siciliana* have not been produced by the same biospecies, but only by close taxa which occupied very different habitats. For that reason it seems impossible to make environmental reconstructions on the base of this genus alone.

Favreina prusensis, occurring monospecifically in flooded karst caves and fissures may have occurred into mixed salinity intertidal cryptic settings, although other reports are from fully marine lagoonal settings. Also in this case different biospecies could be the producers of the same coprolites.

The occurrence of rockforming quantities of internally structured microcoprolites only in certain horizons of the Upper Triassic Lehrberg Beds and in cave fills of the Late Jurassic Ota Limestone together with the preferred preservation of lagoonal microcoprolites in early cemented burrows (Spain) or in submarine caves (Portugal) indicates a strong preservation bias in the record of crustacean microcoprolites. It appears plausible that normally early compaction leads to the loss of internal structures or to the clogging of individual grains to larger irregular particles. We assume that considerable amounts of lacustrine, marginally marine, lagoonal and even deeper water peloidal and micritic limestones may have been derived from the excrementionary activity of ubiquitous crustaceans.

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