Taxonomy and evolution of Kockelella (Conodonta) from the Silurian of Sardinia (Italy)

Enrico Serpagli
Dipartimento di Scienze della Terra
Università di Modena e Reggio Emilia

Carlo Corradini

KEYWORDS – Conodont Kockelella, Taxonomy, New taxa, Silurian, Sardinia.

ABSTRACT – Relatively abundant specimens of Kockelella found in Sardinia permit a revision of many taxa of this important genus and an attempt at a more complete reconstruction of the phylogeny of the whole group.

Besides the two new taxa recently (1998) proposed by us (K. maenniki and K. v. ichnusae), which are here re-described and re-discussed, a new subspecies, K. absidata sardoa of the K. absidata group, is proposed. Furthermore the reconstruction of the apparatus of K. crassa is presented. The biostratigraphic value of the taxa of the genus Kockelella is also stressed.

RIASSUNTO – [Tassonomia ed evoluzione del genere Kockelella (Conodonta) nel Siluriano della Sardegna (Italia)] – Un numero abbastanza elevato di Kockelella provenienti dai terreni siluriani della Sardegna ha permesso di effettuare una revisione di diversi taxa di questo importante genere e di tentare una più completa ricostruzione della filogenesi del gruppo.


INTRODUCTION

Research in Sardinia during the past three decades by one of us (E.S.) and more recently, by a team from Modena University in connection with the preparation of the ECOS VII field trip, has allowed the recovery, from about 70 samples, of conodont elements belonging to several taxa of the genus Kockelella. More precisely, 673 Pa elements, hundreds of Pb (187), M (236), and numerous ramiform elements (918) not yet assigned (Tab. 1), have been identified.

The large number of specimens of Kockelella elements stimulated us to revise the many taxa of this important Silurian genus and to attempt a more complete reconstruction of the phylogeny of the group.

Kockelella, first recorded by Serpagli (1967) from Sardinia, have been recovered from Silurian sediments either in the “Orthoceras limestone” facies (Fluminimaggiore Fm) of the SW or in the “Ockerkalk” facies of the SE. As has been summarised by Ferretti & Serpagli (1996), two distinct types of Silurian successions occur in Sardinia and are similar to the sequences exposed in Bohemia and Thuringia, respectively (see also Corradini & Serpagli, 1999, this volume).

The stratigraphic distribution of Kockelella species is related to the biozonation proposed by Corradini & Serpagli (1998) and discussed further in this symposium volume (Corradini & Serpagli, 1999).

THE PHYLOGENY OF KOCKELELLA

The first reconstruction of the phylogeny of Kockelella was presented by Barrick & Klapper in their authoritative paper of 1976. Subsequently, the problem has been discussed by Kleffner (1994), with regard to some Wenlockian forms, and by Fordham (1991), who, in his cladistic reconstruction of the whole Silurian conodonts, also presented a phylogenetic tree for the Kockelella-Polygnathoides Group (p. 9, Fig. 2d).

It is well known (Sweet, 1988) that the oldest species of genus Kockelella evolved during the middle of Llandovery, probably from species like Ozarkodina abrupta (Aldridge, 1972) and the last species became extinct within the Paleozoic of the Siluric Zone. With the present study, the number of taxa assigned to Kockelella increases from twelve to sixteen. Therefore, we try to contribute to the understanding of the phylogenetic relations within the genus Kockelella as inferred from the Sardinian sequences as well as from the literature.

Three main lineages, mainly based on the Pa element, can be recognised, all originating from the common ancestor K. ranuliformis (Text-fig. 1).

One lineage starts in the latter part of the K. ranuliformis interval Zone with K. walliseri (early forms) evolving from K. ranuliformis by developing a lateral process adjacent of the cusp. K. walliseri lasted up to the K. crassa Zone, without producing any important descendant. In fact, both K. cf. stauros sensu Bischoff,
1986 and *K. corpulenta* became extinct soon in the late Oz. *s. rhenana* Zone. The first became differentiated through a more developed lateral process; the second through a robust blade bearing laterally expanded denticles similar to transverse ridges.

Also in the *K. ranuliformis* interval Zone, a population of *K. ranuliformis* started to develop ridge-like denticles on the blade, giving rise to *K. latidentata*, which become extinct before the end of the succeeding Oz. *s. rhenana* Zone.

In the late Oz. *s. rhenana* Zone, *K. ranuliformis* gave rise to more successful stock, which, after having provided forms with two small lateral processes (*K. amsdeni*), evolved to Pa elements characterised by an even more complex platform, which expanded into a true posterior process (*K. stauros-K. variabilis* Group).

*K. v. variabilis* evolved from *K. stauros* through bifurcation of lateral processes and restriction of the basal cavity to the area under the processes. At the base of the Oz. *exc. hamata* Zone, it produced *K. v. ichnusae*, in which one lateral process became simple and surrounded, and denticles nearly completely fused just anterior to the cusp. The lineage ends with *K. v. ichnusae* in the early *Pol. siluricus* interval (Text-fig. 1).

The third lineage includes three taxa and is characterised by Pa elements in which the cusp is always clearly differentiated from the other denticles. It apparently evolved directly from *K. ranuliformis* by increasing the number of denticles posterior to the main denticle, which gradually become a true cusp. From *K. absidata absidata*, which is the ancestor of this stock, evolved *K. a. sardoa* through development of crowded

---

Text-fig. 1 - Tentative reconstruction of the origin and phylogeny of the genus *Kochelella* based on previous studies (Barrick & Klapper, 1976; Kleffner, 1994) and on the data from Sardinia. Relationship between any branch of the tree and the *K. carrus* stock remain indefinite, as well as with *K. patula* and its possible descendant *A. ploeckensis*. The occurrence of different taxa in Sardinia is shown in dark grey; dotted lines indicate highly speculative connections.
denticles on the anterior process of the Pa element and an anterior constriction of the basal cavity. K. a. sardoa finally produced K. maennikii by developing a long, denticulate lateral process. This lineage starts within the late Oz. s. rhenana Zone and survives into the late Pol. siluricus Zone, therefore including the youngest Kockelella species before the extinction of the genus.

More difficult to place in this phyletic scheme are the K. crassa stock and K. patula stock, which we prefer to consider them as separate groups, apparently not linked each other nor to the main tree.

We believe that K. crassa evolved from forms characterised by a wider platform (Kockelella sp. nov. A Klapper & Murphy, 1975 sensu Bischoff, 1986), which bears a few nodes on its inner side. This form has a more or less rounded-subquadrate outline of the platform, which became almost quadrate in its descendant, K. crassa, in which some variations in the platform of pattern denticles also occurred. This connection is, however, speculative, because of the wide stratigraphic gap between the two taxa.

Even more speculative are the relations between K. patula and its possible descendants, which Fordham (1991) indicates are Kockelella sp. nov. A Klapper & Murphy, 1975 and Ancoradella ploeckensis. Therefore, we prefer to consider this stock as a separate group, apparently not linked to any other, as Barrick & Klapper (1976, fig. 5) did.

Looking at the Kockelella phylogenetic tree, as we have tentatively reconstructed it (Text-fig. 1), some comments can be presented about the evolutionary history of the genus.

After its appearance in the late Llandovery, probably derived from Ozarkodina abrupta-type forms (Sweet, 1988; p.97), the genus Kockelella lasted for about thirteen million years (from 428 Ma to 415 Ma) into the early Ludfordian. The stock flourished with varying success, being twice affected by crises before the final extinction (Text-fig. 1).

The first crisis took place in late Oz. s. rhenana Zone and led to the extinction of nearly all species usually lacking a well defined posterior process (K. ramuliformis, K. latidentata, K. corpalenta, K. amsdeni, K. cf. stauros sensu Bischoff, 1986, Kockelella sp. nov. A Klapper & Murphy, 1975 sensu Bischoff, 1986) as well as K. patula. The second crisis occurred during the K. crassa Zone, just above the Wenlock–Ludlow boundary, and affected K. stauros, Kockelella sp. nov. A Klapper & Murphy, 1975, K. walliseri and K. crassa. The survivors, K. v. variabilis and K. a. absidata, successfully evolved, producing descendants that persisted into the late P. siluricus Zone, when the entire lineage came to an end. No Kockelella has been recorded in sediments younger than the Pol. siluricus Zone (which corresponds to the leinwardinensis (frischti lineari) graptolite Zone), when the closely related taxon, Ancoradella ploeckensis, also became extinct.

**BIOSTRATIGRAPHICAL MEANING**

The biostratigraphic value of kockelellids has been demonstrated by Walliser (1964) and Klapper & Murphy (1976), who used some taxa to name biointervals. With the present study, this value is enhanced because 3 of the new 4 taxa proposed (or re-proposed) here can be of great help in making biostratigraphic determinations. K. crassa was apparently a short-ranged species, limited the basal Gorstian. K. maennikii also ranged briefly together with Pol. siluricus, but didn’t survive through the latest part of the nominate zone. Kockelella v. ibnusa and K. a. sardoa have a slightly lower biostratigraphic significance, being the more successful among the new taxa (Text-fig.1).

**SYSTEMATIC PALEONTOLOGY**

All studied specimens are stored in the Department of Earth Sciences (Palaeontology), Modena University.

**KOCKELELLA ABSIDATA** Barrick & Klapper, 1976

Based on the morphological differences of the Pa and the M elements, two phylogenetically connected subspecies can be distinguished in K. absidata: Kockelella absidata absidata Barrick & Klapper and K. absidata sardoa n. sp. K. a. sardoa evolved from K. a. absidata in late Gorstian time (Text-fig.1). Specimens with intermediate features have been observed in samples from the Oz. exc. hamata and A. ploeckensis zones. It should be pointed out that a further subspecies of this group may be represented by K. ortus ortus (Walliser, 1964) sensu Jeppsson, 1997.

**KOCKELELLA ABSIDATA ABSIDATA** Barrick & Klapper, 1976

Pl. 1, figs. 8-13

Pa element

1957 Spathognathodus cf. primus (Branson & Mehl) - Walliser, pl. 1, figs. 1-2.
1964 Ozarkodina fundamentata (Walliser) - Walliser, pl. 23, figs. 5-9, 11-15, 21 (?) [only].
1969 Ozarkodina fundamentata (Walliser) - Schønlaub, pl. 1, fig. 22.
1971 Ozarkodina fundamentata (Walliser) - Serpagli, pl. 21, fig. 13.
1976 Kockelella absidata n. sp. - Barrick & Klapper, pl. 2, figs. 15-16.
1978 Kockelella absidata Barrick & Klapper - Rexroad, Noland & Pollock, pl. 1, fig. 31.
1983 Kockelella absidata Barrick & Klapper - Wang & Ziegler, fig. 3, n. 5.
1983 Kockelella absidata Barrick & Klapper - Barrick, fig. 18G.
1993 Kockelella abisidata Barrick & Krapper - Schönlaub (in Kritz et al.), pl. 1, fig. 16.
1998 Kockelella abisidata Barrick & Krapper - Serpagli, Corradini & Ferretti, pl. 1.2.1, fig. 8.
1998a Kockelella abisidata Barrick & Krapper - Ferretti, Serpagli, Corradini & Ferretti, pl. 2.2.1, fig. 12; pl. 2.2.2, fig. 5.

**Description** - Pa Elements. Representative specimens have a stout, laterally compressed blade, bearing denticles that are usually more crowded on the anterior part. The anterior process is higher than the posterior one; it is more or less straight and bears up to thirteen closely spaced, laterally compressed denticles. In some specimens, the three or four denticles just anterior to the cusp are fused almost up to their apexes. The posterior process is lower, arched downward and gently incurved; it bears two to six, sometime discrete denticles. The cusp is laterally compressed, reclined and slightly larger than adjacent denticles.

The "spathognathodontus-like" basal cavity is widest beneath the cusp. It narrows gradually towards the posterior end of the specimen, whereas anteriorly, after a gentle constriction just anterior to the cusp, it extends as a narrow groove up to the distal end of the anterior process.

Pb, M, Sa, Sb and Sc Elements. These are (apparently) indistinguishable from the corresponding elements of *K. v. variabilis*.

**Remarks** - The Pa element of *K. a. abisidata* has a more stout appearance, the anterior blade is usually higher than the posterior one, and has the basal cavity a "spathognathodontus-like" outline. Juvenile representatives have a Pa element with a very narrow blade, with densely located denticles, a similar thickness of the anterior and posterior processes and a basal cavity with an "heart-shaped" outline.

M Elements of *K. a. abisidata* differ from the corresponding ones of *K. a. sardoa* in lacking a true anterior process.

**Range** - In Sardinia *K. a. abisidata* appears during the Oz. bohemia Zone, whereas in the literature representatives of this subspecies are known also from the Oz. s. rhenana Zone. The last certain occurrence of *K. a. abisidata* is recorded from the A. ploeckensii Zone. However, a probable (fragmentary) specimen of this taxon has been recovered in the sample GCIU 4, coming from the Pol. siluricus Zone in Sardinia.

**Studied material** - 77 (+2 questionable) Pa and 28 M elements from samples GA 1, GA 2, FRU 0, GCIU 4, SIL 1° 1, SIL 1° 2, SIL 1° 3, GALE BK 50, GALE BK 14, GALE BK 18, GALE BK 23, GALE BK 8, GALE BK 21, SF BK 3, SF 7, SF 9, SF BK 12, SF BK 16, PF 1A, PF 11A, PF 10, PF 1D, PF 1Q, PF 1F, PF 11B and SAD BK 6.

**Kockelella abisidata sardoa** n. ssp.

**Pl. 1, figs. 1-7**

Pa element

1964 *Ozarkodina fundamentata* (Walliser) - Walliser, pl. 23, figs. 16, 18-19, 22-24 [only].

? 1971 *Ozarkodina fundamentata* (Walliser) - Rexroad & Craig, pl. 80, fig. 20 [only].

1972 *Spaethognathodus fundamentatus* Walliser - Link & Druce, pl. 9, figs. 1-11.

1975 Kockelella variabilis Walliser - Klapper & Murphy, pl. 10, figs. 8-11.

1992 Kockelella abisidata Barrick & Krapper - Barrca et al., pl. 11, fig. 5.

1995 Kockelella abisidata Barrick & Krapper - Barrca et al., pl. 4, fig. 11.

1998 Kockelella abisidata Barrick & Krapper - Serpagli, Corradini & Ferretti, pl. 1.2.1, fig. 7.

1998 Kockelella abisidata Barrick & Krapper - Corradini et al., pl. 1.3.1, fig. 16.

M element

1957 *Prioniodina excavata* (Branson & Mehl) - Walliser, pl. 2, fig. 16.

**EXPLANATION OF PLATE 1**

Figs. 1-7 - *Kockelella abisidata sardoa* n. ssp.

1) Paratype, IPUM 25857, sample GCIU 3 (Pol. siluricus Zone); lateral view (a) and lower view (b) of Pa element; x80;

2) Paratype, IPUM 27480, sample GCIU 3 (Pol. siluricus Zone); inner-lateral view of M elements; x66;

3) Holotype, IPUM 27481, sample GCIU 3 (Pol. siluricus Zone); lateral view (a) and lower view (b) of Pa element; x66;

4) Paratype, IPUM 27482, sample SIT 1° 6 (A. ploeckensis Zone); lateral view (a) and lower view (b) of Pa element; x66;

5) Paratype, IPUM 25858, sample SIT 1° 7 (Pol. siluricus Zone); lateral view (a) and lower view (b) of Pa element; x80;

6) Paratype, IPUM 27483, sample SIT 1° 9 (Pol. siluricus Zone); lateral view (a) and lower view (b) of Pa element; x80;

7) Paratype, IPUM 27484, sample SIT 1° 10 (Pol. siluricus Zone); lateral view of Pa element; x80.

Figs. 8-13 - *Kockelella abisidata abisidata* Barrick & Krapper, 1976.

8) IPUM 25861, sample PF 11B (Oz. exc. hamata Zone); lateral view of Pa element; x80;

9) IPUM 27476, sample GALE BK 18 (K. crassa Zone); lateral view (a) and lower view (b) of Pa element; x66;

10) IPUM 27479, sample PF 1Q (A. ploeckensis Zone); lateral view of Pa element; x80;

11) IPUM 25860, sample PF 1Q (A. ploeckensis Zone); lateral view of Pa element; x70;

12) IPUM 27477, sample SF BK 3 (Oz. bohemia Zone); lateral view (a) and lower view (b) of Pa element; x66;

13) IPUM 27478, sample PF 1D (Oz. exc. hamata Zone); lateral view (a) and lower view (b) of Pa element; x66.
E. SERPAGLI, C. CORRADINI, TAXONOMY AND EVOLUTION OF KOCHELELLA

Pl. 1
Holotype – the specimen illustrated on Pl. 1, Fig. 3a,b, IPUM 27481.

Paratypes (figured) – IPUM 25857-25858, 27480, 27482-27484.

Locus typicus – Genna Ciuciu section, close to the Silius village, South East Sardinia, Italy.

Stratum typicum – GCIU 3.

Derivatio nominis – Latin sardous, from Sardinia.

Diagnosis – The Pa element is characterised by a laterally compressed, densely denticulated blade. No significant differences exist in thickness between the anterior and posterior part of the blade. The "heart-shaped" basal cavity has a sharp constriction just anterior to the cusp and gradually tapers posteriorly.

Description – Pa element. Representative specimens have a very narrow, laterally compressed blade bearing crowded denticles. The anterior process is more or less straight and bears up to twelve closely spaced laterally compressed denticles. The short posterior process is arched downward and gently incurved; it bears two to five closely spaced denticles. The height of the anterior and posterior parts of the blade is similar. The cusp is laterally compressed, reclinod and slightly larger than the adjacent denticles. The basal cavity is shallow and slightly flared on both sides below the cusp. The outer flare of the cavity is usually better developed and may bear a small denticle. The basal cavity has a "heart-like" shape, because it tapers gradually towards the posterior end of the unit, whereas, after a more or less sharp constriction just anterior to the cusp, it continues as a narrow groove below the anterior process.

M element (Pl. 1, fig. 2). Specimens are slightly curved and sometimes arched, with a long stout, biconvex cusp, which is gently curved and slightly twisted to the posterior. The posterior process is twisted and bears up to nine laterally compressed, reclinod, discrete denticles. The denticles closer to the cusp are smaller than others, and more densely spaced. A short anterior process is deflected outwards and, in some specimens, descends downwards from the cusp. This process usually bears two denticles. The basal cavity is widest below the cusp and has a prominent flaring on the inner side of the element, and opens somewhat to the posterior.

Pb, Sa, Sb and Sc elements. These elements are apparently indistinguishable from the corresponding elements of K. v. variabilis and K. a. absidata

Remarks – Pa element. The Pa element of K. absidata sardoa differs from that of K. a. absidata in three main features:
- the general outline of the blade: in K. a. absidata the anterior process is higher than the posterior one, and the blade has a more stout appearance;
- the outline of the basal cavity: in K. a. absidata tapers anteriorly more gently whereas in K. a. sardoa it has a "heart-like" shape;
- the pattern of denticulation: in K. a. sardoa denticles are closely spaced on both processes, whereas in K. a. absidata they may be less crowded, up to discrete, on the posterior process.

K. absidata sardoa is similar to K. maenniki, and differs from it mainly in the lack of lateral processes.

M element. The M element of K. a. sardoa differs from the corresponding element of K. a. absidata in having a true anterior process; it is different from the M element of K. maenniki because in the latter the denticles are closely spaced and the posterior process is strongly arched.

K. a. sardoa has excellent biostratigraphical value, spanning an interval from the base of the A. pleckensis Zone to within the Pol. siliacus Zone. In fact all our material, as well as the specimens reported on the synonym list, is from this interval.

The specimens illustrated from Cellon by Walliser (1964) as Oz. fundamentata and here reported in the

EXPLANATION OF PLATE 2

Figs. 1-9 - Kockeilella crassa (Walliser 1964).
1) IPUM 27488, sample SAD BK 2 (K. crassa Zone); upper view (a) and lower view (b) of Pa element; x66;
2) IPUM 25841, sample GALE BK 18 (K. crassa Zone); upper view (a) and lower view (b) of Pa element; x80;
3) IPUM 26137, sample SAD BK 2 (K. crassa Zone); upper view (a), lower view (b) and lateral view (c) of Pa element; x80;
4) IPUM 27489, sample SF 7 (K. crassa Zone); upper view of Pa element; x90;
5) IPUM 25842, sample GALE BK 18 (K. crassa Zone); upper view (a), lower view (b) and upper-lateral view (c) of Pa element; x60;
6) IPUM 25843, sample PF 1A (K. crassa Zone); upper view of Pa element; x80;
7) IPUM 25840, sample SAD BK 2 (K. crassa Zone); upper view (a), lower view (b) and upper-lateral view (c) of Pa element; x80;
8) IPUM 25917, sample PF 1A (K. crassa Zone); lateral view of Pb element; x85;
9) IPUM 25916, sample PF 11A (K. crassa Zone); lateral view of Pb element; x80.
Table 1 – Distribution of the different species of *Kockeleva* in samples from Sardinia. Locality abbreviations: SE Sardinia: GA=Genna Arrela, FRU=Monte Fruccas, GCU=Genna Ciuciucu, SIL=P.=Silius P., RMC=Riu Murru de Callus, SBF=San Basilio Fenigu; SW Sardinia: GALE=Galemmu, SF=Sentiero Flumini, CB III=Corti Baccas 3°, PF=Perd’e Fogo, ARG=Argiola, FTM=Fontanamare, SAD=San’tAntonio Donigala.
synonymy list, come from the *A. ploeckensis* (Pl. 23, figs. 16, 18) or from the *Pol. siluricus* Zone (Pl. 23, figs. 19, 22-24); the Australian specimens figured by Link & Druce (1972) are from the same stratigraphical interval. The specimens from Nevada, recorded by Klapper & Murphy (1975) as O. (= Pb) elements of *K. variabilis*, come from the samples where *Pol. siluricus* and/or *Oz. confluen* are also present.

Range — From the base of the *A. ploeckensis* Zone to the *Pol. siluricus* Zone.

**Studied material** — 82 (+2 questionable) Pa and 32 M elements from samples GA 1, GA 2, GA 4, GCIU 0, GCIU 3, GCIU 5, SIL 1° 1, SIL 1° 4, SIL 1° 5, SIL 1° 6, SIL 1° 7, SIL 1° 9, SIL 1° 10 SIL 1° 11, SIL 1° 12, RMC 1G; RMC 1D, GALE BK 13, PF 11B, PF 1H, PF 5, FTM 2, SAD BK 3A and SAD BK 6.

**Kockelella crassa** (Walliser, 1964)

*Pl. 2, fig. 1-9*

**Pa element**

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1964</td>
<td><em>Kockelella variabilis</em> Walliser - WALLISER, 16, figs. 2, 8, 11 (only).</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td><em>Kockelella variabilis</em> Walliser - IGO &amp; KOIKE, 10, pl. 3, figs. 6-9.</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td><em>Kockelella variabilis</em> Walliser - SCHÖNLAUB, pl. 1, fig. 16.</td>
<td></td>
</tr>
<tr>
<td>1975</td>
<td><em>Kockelella variabilis</em> Walliser - KLAPPER &amp; MURPHY, 9, fig. 10.</td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td><em>Kockelella variabilis</em> Walliser - WANG &amp; ZIEGLER, pl. 3, fig. 7.</td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td><em>Kockelella variabilis</em> Walliser - BARCA et al., pl. 10, fig. 1.</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td><em>Kockelella variabilis</em> Walliser - SCHÖNLAUB (in KRIS et al.), pl. 1, fig. 15.</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td><em>Kockelella circuquadra</em> n.sp. - SERPAGLI &amp; CORRADINI, pp. 79-80, pl. 1, figs. 3 a-c, 4. 7.</td>
<td></td>
</tr>
<tr>
<td>1998a</td>
<td><em>Kockelella circuquadra</em> Serpagli &amp; Corradini - FERRETTI, CORRADINI &amp; SERPAGLI, pl. 2.2.1, fig. 15; pl. 2.2.2, fig. 15.</td>
<td></td>
</tr>
</tbody>
</table>

**Pb element**

<table>
<thead>
<tr>
<th>Year</th>
<th>Reference</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1964</td>
<td><em>Ozarkodina crassa</em> n.sp. - WALLISER, p. 55, pl. 7, fig. 9; pl. 24, figs. 14-17.</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td><em>Ozarkodina crassa</em> Walliser - FAHRAEUS, p. 12, tab. 1, pl. 2, fig. 5.</td>
<td></td>
</tr>
<tr>
<td>1974</td>
<td><em>Ozarkodina crassa</em> Walliser - WALMSLEY, ALDRIDGE &amp; AUSTIN, fig. 3.</td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>&quot;<em>Ozarkodina crassa</em>&quot; Walliser - BARRICK &amp; KLAPPER, pl. 2, figs. 12, 13.</td>
<td></td>
</tr>
<tr>
<td>1971</td>
<td><em>Ozarkodina crassa</em> Walliser - SERPAGLI, p. 89, pl. 21, figs. 10, 11.</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td><em>Ozarkodina crassa</em> Walliser - SCHÖNLAUB (in KRIS et al.), pl. 1, figs. 17, 18.</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td><em>Polygnathoides crassus</em> (Walliser, 1964) - FERRETTI, CORRADINI &amp; SERPAGLI, pl. 2.2.1, fig. 7; pl. 2.2.2, fig. 8.</td>
<td></td>
</tr>
</tbody>
</table>

**Diagnosis** — Pa element (after Serpagli & Corradini, 1998). The Pa element is characterised by a widely expanded, almost symmetrical, basal cavity with a quadrate-subquadrate outline. The platform bears three-five denticles on each side (up to nine in larger specimens), usually arranged in an X pattern. A portion of platform free of denticles occurs on both sides of main blade, therefore no ridge connects the cusp with the first denticle of the platform. Posterior process is short and generally straight. The length/width ratio of the whole element is usually very high (avg. close to 2).

**Pb element** (after Walliser, 1964). Ozarkodiniform element characterised by a stout cusp, triangular in cross section, and by a massive blade, sometimes flaring on one side of the platform.

**Description** — Pa element. The anterior blade is long and straight and bears 8 to 9 closely spaced erect denticles, which are larger in size near the distal part of the blade except for the last one, which usually is very small. In the largest specimens, denticles of the middle part of the blade are partially fused. The cusp is only slightly larger than the adjacent denticles. The posterior blade is short and generally straight and bears 3 to 5 closely spaced sub-erect denticles. The basal cavity is widely expanded and nearly symmetrical with an almost quadrate outline. The upper surface of the platform bears three to five denticles on each side; in larger specimens the number may increase up to eight to nine. Denticles are usually arranged irregularly on one side, whereas on the other they are almost aligned close to the outside margin, parallel to the blade. No ridge is present between the cusp and the nearest platform denticle; thus a smooth (unornamented) portion of the platform lies on each side of the blade.

**Pb element.** The cusp is stout, recliné, usually triangular in cross section with the anterior and the posterior margins very sharp. The anterior process is slightly longer than the posterior one and bears up to six (exceptionally seven) stout, biconvex denticles; the posterior process is slightly lower than the other and carries up to four, usually discrete, denticles. One side of the blade is slightly expanded in connection of the cusp; this flared area sometimes may bear a knob (pl. 3, fig. 8-9) or even can develop into a small lateral process (*i.e.:* Walliser, 1964, pl. 24, fig. 17). The basal cavity extends as a groove under both processes and appears asymmetrical developed under the cusp.

**M, Sa, Sb and Sc elements.** No description of these elements is supplied, owing to the poorness of the available material. However, they are apparently similar to those described under *K. v. variabilis*.

**Remarks** — The idea that *Oz. crassa* Walliser, 1964 represents the Pb element of an apparatus including as Pa element *K. circuquadra* Serpagli & Corradini, 1998
has been kindly suggested to us by Jim Barrick (pers. comm. 11/03/1999). It follows that, according to the priority laws, the species must be named *Kockelella crassa* (Walliser, 1964).

Pa elements belonging to *K. crassa* differ from both *K. v. variabilis* and *K. patula* in the general shape of the basal cavity. Sinuses in the margin of the cavity of this species are not developed as between the secondary processes of both of the latter species. Further differences are:

- in *K. v. variabilis* is the basal cavity is usually less expanded and the length/width ratio is lower;
- *K. patula* has also a large platform, but the basal cavity is clearly asymmetrical (non quadrate) with well developed secondary processes; furthermore, the posterior process is typically curved.

*K. crassa* appears to have good biostratigraphical value, being limited to the basal Ludlow; in fact representatives of *K. crassa* have been reported from the lowermost Gorstian, only.

Three Pa elements recorded at Cellon as *K. variabilis* are here reported in the synonym list as *K. crassa* on the basis of camera lucida drawings of the basal cavity kindly supplied by O. Walliser in December 1997. These specimens are from level C.15B1, i.e. the base of the *K. crassa* Zone (see Corradini & Serpagli, 1999, this volume). The specimens from Bohemia (Schönlauß, 1993 in Krz et al.), either Pa or Pb, are from the same zone, being reported from the *C. colonus* graptolite Zone, which is equivalent to the *K. crassa* Zone. The Pa elements from Malaya (Igo & Koike, 1968) and from Nevada (Klapper & Murphy, 1975) fit in the same interval.

The 13 Pa elements recorded in Sardinia by Serpagli (1971; tab.1, p.80) as *Kockelella variabilis* from samples SF 7 and SF 8 (but not illustrated) and occurring with the Pb element “Ox.” *crassa* actually belong to *K. crassa*.

**Range** – *K. crassa* Zone.

**Studied material** – 36 (+1 questionable) Pa elements and 7 Pb elements from samples GALE BK 18, GALE BK 50, SF BK 3, SF BK 17, SF 7, SF 8, PF 1A, PF 11A and SAD BK 2.

---

**EXPLANATION OF PLATE 3**

1) Paratype, IPUM 25846, sample GCIU 3 (*Pol. siluricus* Zone); upper view (a), upper-lateral view (b) and lower view (c) of Pa element; x80;
2) Paratype, IPUM 25848, sample GCIU 2 (*Pol. siluricus* Zone); upper-lateral view of Pa element; x80;
3) Paratype, IPUM 25850, sample GCIU 3 (*Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x80;
4) Paratype, IPUM 27485, sample GA 4 (*Pol. siluricus* Zone); upper view (a) and upper-lateral view (b) of Pa element; x80;
5) Paratype, IPUM 25853, sample PF 11B (*Pol. siluricus* Zone); lateral view of Pa element; x80;
6) Paratype, IPUM 25848, sample GCIU 3 (*Pol. siluricus* Zone); upper view of Pa element; x80;
7) Paratype, IPUM 25849, sample GCIU 3 (*Pol. siluricus* Zone); upper view of Pa element; x80;
8) Paratype, IPUM 27486, sample SIL P.9 (9 *Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x66;
9) Paratype, IPUM 26141, sample PF 1H (*Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x80;
10) Holotype, IPUM 25845, sample GCIU 3 (*Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x80;
11) Paratype, IPUM 25847, sample GCIU 3 (*Pol. siluricus* Zone); upper view of Pa element; x80;
12) Paratype, IPUM 27487, sample GCIU 3 (*Pol. siluricus* Zone); inner-lateral view of M element; x80.
conspicuous, usually curved on one side and arched downward. Cusp well developed and differentiated from the other denticles.

**Description** — Pa element is slender, slightly curved and arched. Blade is very narrow and laterally compressed; its anterior part is usually straight and bears from 8 to 12 closely spaced, laterally compressed denticles. The conspicuous posterior blade is usually curved to one side and arched downward; it bears up to 6 closely spaced, laterally compressed denticles.

The slightly reclined cusp is well developed, always separable from the other denticles and located on the posterior third of the unit.

Platform is strongly asymmetrical and typically is strongly developed on outer side, where a simple long process bears up to five (commonly three) aligned denticles, which are usually slightly proclined. The inner side of the platform is usually smooth, but in some specimens a single small denticle may occasionally be present. The basal cavity is wide below the platform and extends as a narrow groove to the ends of the processes.

M element (Pl. 3, fig. 12). Specimens are slightly curved and usually arched, with a long, stout, biconvex cusp. The cusp is gently curved and slightly twisted to the posterior. The posterior process, usually strongly arched and twisted, bears up to ten laterally compressed, reclined, closely spaced denticles. An anticusp-like anterior process bears two or three laterally compressed denticles crowded adjacent to the cusp. The basal cavity has a prominent flaring of margin on the inner side of the unit and opens somewhat to the posterior.

Pb, Sa, Sb and Sc elements. These elements are apparently indistinguishable from the corresponding elements of K. *v. variabilis* and *K. a. abisidata.*

**Remarks** — Pa element. The Pa element of *K. maenniki* differs from that of *K. abisidata sardoa* by the occurrence of a lateral process; it is unlike *K. stauros* Barrick & Klapper in having a typically asymmetrical basal cavity and a single lateral process. The outer lateral process is usually anteriorly bent, but in few specimens it is perpendicular to the blade, or even posteriorly directed. Some juvenile specimens have a *"spathognathodus-like" appearance and, if denticles on lateral process are not yet developed, is not easy to separate them from true "Spahtognathodus".*

M element. The M element of *K. maenniki* is very similar to that of *K. a. sardoa*, but has a more arched posterior process and a denticulate anticusp instead of a real anterior process.

*K. maenniki* has good biostratigraphical value, being limited to the early-middle part of the *Pol. siluricus* Zone. In fact, all our material, as well as the specimens reported on the synonymy list, are from this interval.

Specimens of *K. maenniki* from the "Nördliche Grauwackenzone" (Austria) have been recorded in samples in which *Pol. siluricus* or *Oz. confluent* have been found (Flajs & Schönlaub, 1976, pl. 4, figs. 17-19). Also, the specimen illustrated by Mänik & Malkowski (1998, pl. 2, fig. 12) from the *Pol. siluricus* Zone in the Goldap Core (Poland), and identified as *Kockeella* sp., is in reality *K. maenniki.*

**Range** — Early-middle part of the *Pol. siluricus* Zone.

**Studied material** — 73 (+1 questionable) Pa and 19 M elements from samples GA 3, GA 4; GCIU 0, GCIU 2, GCIU 3; GCIU 5; SIL 17, SIL 18, SIL 19, SIL I 12; RMC 1B, RMC 1C; GALE BK 13; CB II-BK 1a; PF 1H, PF 5; FTM 1 and FTM 2.

**Kockeella ranuliformis** (Walliser, 1964)

Pl. 7, fig. 10

**Pa element**

1964 *Spahtognathodus ranuliformis* WALLISER, p. 82, tav. 6, fig. 9; pl. 22, figs. 3-7.

1976 *Kockeella ranuliformis* (Walliser) - BARRICK & KLAPPER, p. 76, pl. 2, figs. 1-11.

1983 *Kockeella ranuliformis* (Walliser) - BARRICK, fig. 18L.

1995 *Kockeella ranuliformis* (Walliser) - SIMPSON & TALENT, p. 135, pl. 6, figs. 2-7 (only) (zuw. syn.).

1998a *Kockeella ranuliformis* (Walliser) - CORRADINI, FERRETTI & SERPAGLI, pl. 3.3, fig. 4a, b.

**Remarks** — The round basal cavity at the posterior end of the Pa element, and the absence of lateral processes are the main features of this species. No more

---

**EXPLANATION OF PLATE 4**


1) Paratype, IPUM 25839, sample PF 11B (*Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x80.
2) Paratype, IPUM 27490, sample FTM 2 (*Pol. siluricus* Zone); upper view (a) and lower view (b) of Pa element; x66.
3) Paratype, IPUM 25836, sample SIL P 5 (*A. plocenhensis* Zone); upper view (a) and lower view (b) of Pa element; x80.
4) Paratype, IPUM 27491, sample SBF 5 (*A. plocenhensis* Zone); upper view of Pa element; x66.
5) Holotype, IPUM 25834, sample SIL P 5 (*A. plocenhensis* Zone); upper view (a), lower view (b) and upper-lateral view (c) of Pa element; x60.
6) Paratype, IPUM 25838, sample PF 1Q (*A. plocenhensis* Zone); upper view (a) and lower view (b) of Pa element; x60.
7) Paratype, IPUM 25835, sample SBF 5 (*A. plocenhensis* Zone); upper view of Pa element; x80.
E. SERPAGLI, C. CORRADINI, TAXONOMY AND EVOLUTION OF KOCKELELLA

PL. 4
information can be supplied with the scarce available material.

Range – From the Pt. celloni Zone (Pt. am. angulatus Subzone) to Oz. s. rhenana Zones

Studied material – 2 Pa elements from sample ARG C.

KOCKELELLA STAUROS Barrick & Klapper, 1976

Pl. 7, figs. 8-9

Pa element

1976 Kockelella stauros Barrick & Klapper, p. 76, pl. 3, figs. 1-11.
1983 Kockelella stauros Barrick & Klapper - Barrick fig. 18N.
1994 Kockelella stauros Barrick & Klapper - KLEFFNER, fig. 10.20.

Remarks – The few specimens from Sardinia come from the late Oz. bohemia Zone and from the early K. crassa Zone.

According to the left-hand columns of the Silurian Times n.3 (1995), a K. stauros Zone, equivalent to the colonus-nilsoni grapholite interval, is claimed to be used for global correlations in the Early Ludlow. However we believe that true K. stauros is in North America limited to the Homerian (Barrick & Klapper, 1976), whereas in Sardinia it reaches the lowermost Gorstian, occurring in few samples with K. crassa. The "stauros-like" specimens often occurring in the Oz. exc. hamata and A. ploeckensis zones are actually juvenile specimens of K. variabilis variabilis (text-fig. 2).

Range – From the Oz. s. sagitta Zone to the lowermost K. crassa Zone.

Studied material – 8 Pa elements in SF BK 3; SF BK 17; GALE BK 18, GALE BK 40 and GALE BK 50.

KOCKELELLA VARIABILIS Walliser, 1957

Based on the morphology of the Pa element, two subspecies were recognised in K. variabilis: Kockelella variabilis variabilis Walliser and K. variabilis ichnusae Serpagli & Corradini.

KOCKELELLA VARIABILIS VARIABILIS Walliser, 1957

Pl. 5, figs. 1-13; pl. 6, figs. 1-9; pl. 7, figs. 1-7

Pa element

1957 Kockelella variabilis n.sp. Walliser, p. 35, pl. 1, figs. 3-10.
1962 Kockelella variabilis Walliser - ETHINGTON & FURNISH, p. 1270, pl. 172, figs. 4-5.
1962 Kockelella variabilis Walliser - REICHESTEIN, p. 538, fig. 2.
1964 Kockelella variabilis Walliser - Walliser, p. 35, pl. 16, figs. 3-4, 6, 9-10, 13, 14-15.
1965 Kockelella variabilis Walliser - Van den Boogaard, p. 34-36, figs. 2-5.
1971 Kockelella variabilis Walliser - Serpagli, pl. 22, fig. 13.
1972 Kockelella variabilis Walliser - Link & Druce, pl. 4, figs. 1-4-5.
1972 Kockelella variabilis Walliser - Vai, pl. 32, figs. 2, 7.
1975 Kockelella variabilis Walliser - Klapper & Murphy, pl. 9, figs. 5, 6-9, 11; pl. 10, figs. 1-7.
1976 Kockelella variabilis Walliser - Barrick & Klapper, pl. 3, figs. 12-17.
1980 Kockelella variabilis Walliser - Aldridge, figs. 8-11.
1981 Kockelella variabilis Walliser - UYENO, pl. 8, figs. 9-10.
1983 Kockelella variabilis Walliser - Barrick, fig. 18f.
1983 Kockelella variabilis Walliser - Wang & Ziegler, pl. 3, fig. 7.
1985 Kockelella variabilis Walliser - Aldridge, pl. 3.4, fig. 5.
1998 Kockelella variabilis variabilis Walliser - Serpagli, Corradini & Ferretti, pl. 1.2.2, fig. 13.

EXPLANATION OF PLATE 5

In order to show variation from juvenile to adult Pa elements, all specimens illustrated in this plate come from the same sample and have the same magnification. Two additional specimens belonging to the same growing series are illustrated in the next plate (Pl. 6, figs. 8-9).

Figs. 1-13 - Kockelella variabilis variabilis Walliser, 1957. All specimens from sample GALE BK 23 (K. n. variabilis Zone); x66.
1) IPUM 27493/1; upper view of Pa element;
2) IPUM 27493/2; upper view of Pa element;
3) IPUM 27493/3; upper view of Pa element;
4) IPUM 27493/4; upper view of Pa element;
5) IPUM 27493/5; upper view of Pa element;
6) IPUM 27493/6; upper view of Pa element;
7) IPUM 27493/7; upper view of Pa element;
8) IPUM 27493/8; upper view of Pa element;
9) IPUM 27493/9; upper view of Pa element;
10) IPUM 27493/10; upper view (a) and lower view (b) of Pa element;
11) IPUM 27493/11; upper view (a) and lower view (b) of Pa element;
12) IPUM 27493/12; upper view (a) and lower view (b) of Pa element;
13) IPUM 27493/13; upper view (a) and lower view (b) of Pa element.
process on both sides of the blade in the posterior part of the element.

The anterior process is long, straight and relatively thick; it bears up to 11 laterally compressed denticles; they are very closely spaced (up to fused) proximally, whereas one or two, stout, high and discrete, occur in the distal part; the blade ends with one or two short, small denticles.

The denticles placed where the ridges of the lateral processes meet the junction of the anterior and posterior processes can be considered as the cusp, which, however, does not differ in size from the adjacent denticles.

The posterior process is short and curved and bears up to five laterally compressed, closely spaced, sometime partially fused denticles.

Bifurcated lateral processes are present on both sides of the blade. They are connected by a narrow ridge. The outer lateral process is usually more developed than the inner one; it bears two ridges of 3-5 denticles. The angle between these ridges is up to 90°. In adult specimens these ridges protrude out of the platform, generally the posterior one is better developed than the other. In few specimens these ridges may branch further. The denticle pattern on the inner lateral process is extremely irregular, when the denticles form two short ridges bearing 1-3 denticles each.

The basal cavity is wide and slightly asymmetrical, having a heart-shaped (subtriangular) outline in small specimens and a polygonal (approximately subrectangular) in large ones, owing to the strong development of the posterior ridge of the outer lateral process. The basal cavity extends as a deep groove under the anterior blade.

**Pb element** (Pl. 6, fig. 6; pl. 7, fig. 5). Cusp is large biconvex and reclined. Anterior and posterior processes are more or less equal in length and bear six to eight slightly compressed denticles. The anterior process is usually more robust than the posterior one and denticles on it may be partially fused. The basal cavity extends as a groove under both processes and appears under the cusp as a rounded flaring expansion, definitely larger on the outer side. The anterior groove is narrower and deeper than the posterior one.

---

**Amended diagnosis**—The Pa element [of *K. variabilis variabilis*] is characterised by lateral processes typically branched (adult specimens) and a length/width ratio usually very low (avg. close to 1.6). The wide, slightly asymmetrical basal cavity, has a heart-shaped (subtriangular) outline in small specimens and a polygonal (approximately subrectangular) in large ones, and is generally confined to the area under the lateral processes and posterior blade.

**Description**—Pa element. Representative specimens are straight to slightly curved, with a lateral bifurcated process on both sides of the blade in the posterior part of the element.

**SA element**

1957 *Prioniodina cf. armata* (Hinde) - WALLISER, pl. 2, fig. 21 [only].
1964 *Neoprionodus multiformis* n.sp. WALLISER, pl. 29, figs. 14, 17-18, 21-22, 25 [only].
1971 *Neoprionodus multiformis* WALLISER - SERPAGLI, pl. 22, fig. 9.
1992 *K. variabilis* WALLISER, M element - BARCA et al., pl. 10, fig. 2.

**Sb element**

1964 *Lonchodina greilingi* WALLISER - WALLISER, pl. 44, pl. 9, fig. 7; pl. 30, figs. 7-9.

**Sc element**

1957 *Ligonodina diversa* n.sp. WALLISER, p. 36, pl. 2, figs. 11, 13-14 [only].
1964 *Ligonodina salopia* Rhodes - WALLISER, pl. 41-42, pl. 8, fig. 9; pl. 32, fig. 5, 10.

---

**EXPLANATION OF PLATE 6**

Figs. 1-9 - Kockeella variabilis variabilis Walliser 1957. All specimens from sample GALE BK 23 (K. v. variabilis Zone).

1) IPUM 27493/21; inner-lateral view of Sc element; x50;
2) IPUM 27493/22; inner-lateral view of Sc element; x66;
3) IPUM 27493/18; inner-lateral view of M element; x50;
4) IPUM 27493/19; posterior view of Sa element; x50;
5) IPUM 27493/20; posterior view of Sb element; x66;
6) IPUM 27493/17; inner-lateral view of Pb element; x50;
7) IPUM 27493/14; upper view (a) and lower view (b) of Pa element; x66;
8) IPUM 27493/15; upper view (a) and lower view (b) of Pa element; x66;
9) IPUM 27493/16; upper view (a) and lower view (b) of Pa element; x66.
M element (pl. 6, fig. 3; pl. 7, fig. 7). Specimens are slightly curved with a long stout, biconvex cusp, which is gently curved and slightly twisted to the posterior. The posterior process bears six to nine erect, discrete denticles, (sub)round in cross section. A true anterior process is missing, whereas a short anticusplike extension has been observed in some specimens. Sometimes, a small, partially fused with the cusp denticle may be present on the anterior margin; also a second denticle has been occasionally observed. The basal cavity opens somewhat to the posterior and has a prominent flaring margin on the inner side of the element.

Sa element (pl. 6, fig. 4). Specimens are symmetrical with a slender, long cusp, sub-oval in cross section, which sometimes bears a narrow keel on both lateral sides. The two straight, equal, lateral processes are directed sharply downwards from the cusp and diverge at an angle close to 90°. Each process bears about six round, erect, discrete denticles. A more or less developed posterior expansion of the basal cavity, in form of a rounded lip, is always present.

Sb element (Pl. 6, fig. 5; pl. 7, fig. 4). Specimens are asymmetrical and bowed, with two arched processes of different length. The cusp is long, slender and reclined, sometimes bearing a narrow keel on both lateral sides. The posterior process, longer than the anterior one, arches sharply downwards from the cusp and is slightly incurved; it bears 6 to 7 round, erect, discrete denticles. The anterior process, somewhat twisted, forms an angle of about 90° with the posterior and bears 4 to 6 denticles. The processes lie on different planes, forming an angle up to 90° degrees in strongly bowed specimens. The basal cavity is expanded posteriorly as a round protrusion that gradually closes towards the end of the processes.

Sc element (Pl. 6, figs. 1-2; pl. 7, fig. 6). Specimens have a long, stout reclined cusp, sometimes bearing a narrow keel in the anterior part of the inner side. The cusp has a sub-oval cross section near the base, whereas in the upper part it shows a flat anterior margin. The posterior process is long, sometimes slightly arched and turned towards the outer side, bearing up to twelve reclined, discrete denticles, rounded in cross section. Antero-lateral process forms a more or less square angle with the posterior process and descends sharply downward from the cusp at different angles; it bears five to seven discrete, slightly posteriorly bent denticles, rounded in cross section.

Text-fig. 2 — Camera lucida drawings of some specimens of K. v. variabilis arranged in sequences to show gradual morphologic changes from juvenile to adult specimens. Each sequence is based on specimens of the same sample to point out that some juvenile specimens can be wrongly referred to K. staturos. Magnification: x40. A) sample GALE-BK 8 (A. ploeckensis Zone), "Orthoceras lin." of the Flumimimaggiore Fm., A. ploeckensis Zone, SW Sardinia; the fourth and eighth specimens have been drawn reversed. B) sample SIL P 4, (A. ploeckensis Zone), "Ockerkalk" facies, SE Sardinia.
Remarks – Pa element. In several samples from Sardinia, from both the Ockerkalk and Orthoceras limestone facies, it is possible to recognise complete sequences from juvenile to adult specimens, showing all intermediate stages (Text-fig. 2; pls. 5, 6). Sequences begin with “Spathognathodus-like” specimens without any denticulate lateral process (Text-fig. 2, A, B; pl. 5, fig. 1), showing only a crest on one or both sides of the blade, followed by “stauros-like” specimens with one or two denticles on each side (Text-fig. 2, A, B; pls. 5, figs. 2-3). The sequence continues, after further intermediate stages, with specimens bearing one branched lateral process (Text-fig. 2, A, B; pls. 5, figs. 4-5) and ends with specimens bearing branched lateral processes on both sides of the element (Text-fig. 2, A, B; pls. 5, figs. 8-9).

The Pa element of K. variabilis differs from that of K. ichnusae mainly in having a more symmetrical platform, no rim on its margin and by the lack of a true crest produced by some fused denticles anteriorly to the cusp. Furthermore, in adult specimens of K. variabilis both lateral processes are branched and the length/width ratio in K. ichnusae is higher. Finally, in lower view, the posterior process of K. variabilis is apparently undifferentiated from the main part of the basal cavity, whereas in K. ichnusae it is always recognisable because the cavity narrows posteriorly.

However, intermediate forms between K. variabilis and K. ichnusae have been observed in samples coming from the K. variabilis and the Os. exc. hamata Zones.

The Pa element of K. variabilis differs from the equivalent of K. crassa in the shape of the basal cavity, which is usually less expanded and irregularly developed. Furthermore, in K. variabilis lateral processes are always well developed and a ridge usually connects the cusp with the nearest denticle on the platform (no “unnamed area” exists close to the blade).

M element. The M element of K. variabilis never possesses an anterior process, differing, therefore, from the same elements of K. a. sardoa and K. maenniki.

Sc element. We believe that this element is much more similar to Ligonodina salopia (sensa Walliser, 1964, but not to L. salopia sensu Rhodes, 1953), than to L. silurica Branson & Mehl (sensa Walliser, 1957).

Range – From the late K. crassa Zone to the top of the A. pliocenensis Zone.

Studied material – 308 (+1 questionable) Pa elements from samples GA 2, FRU A, FRU 0, FRU B, SIL 1° 1, SIL 1° 2, SIL 1° 3, SIL 1° 4, SIL 1° 5, SIL 1° 6, RMC 0, RMC 1, RMC 1A, GALE BK 40, GALE BK 23, GALE BK 8, SF 9, SF 12, SF BK 12, PF BK G, PF 9, PF 10, PF 1D, PF 0, PF 1Q and PF 11B.

KOCKELELLA VARIABILIS ICHNUSAE
Serpaglì & Corradini, 1998
Pl. 4, fig. 1-7

Pa element
1964 Kockelella variabilis Walliser - Walliser, pl. 16, figs. 11, 51, 7, 12.
1971 Kockelella variabilis Walliser - Rexroad & Craig, pl. 82, figs. 8-10.
1971 Kockelella variabilis Walliser - Rexroad & Nicolli, pl. 2, fig. 8.
1972 Kockelella variabilis Walliser - Link & Druce, pl. 3, figs. 11, 12, 15, 16; text-fig. 21.
1972 Kockelella variabilis Walliser - Vai, pl. 32, fig. 1.
1975 Kockelella variabilis Walliser - Schonlau & Zezula, pl. 1, fig. 1.
1976 Kockelella variabilis Walliser - Birner, pl. 2, fig. 3.
1977 Kockelella variabilis Walliser - Cooper, pl. 17, figs. 1, 5.
1980 Kockelella variabilis Walliser - Schonlau, pl. 6, fig. 1.
1995 Kockelella variabilis Walliser - Barca et al., pl. 4, fig. 15.
1998 Kockelella variabilis ichnusae n.sp. Serpagli & Corradini, figs. 80-82, pl. 1, figs. 1a-c, 2.
1998 Kockelella variabilis ichnusae Serpagli & Corradini - Serpagli, Corradini & Perretti, pl. 1.2.1, fig. 10.
1998a Kockelella variabilis ichnusae Serpagli & Corradini - Corradini et al., pl. 1.3.1, fig. 14.
1998a Kockelella variabilis ichnusae Serpagli & Corradini - Perretti, Corradini & Serpagli, pl. 2.2.1, fig. 16; pl. 2.2.2, fig. 14.
1998 Kockelella variabilis Walliser - Mannik & Malkowski, pl. 2, fig. 5.
1998 Kockelella aff. variabilis - Mannik & Malkowski, pl. 2, fig. 10.

Holotype – The specimen illustrated by Serpagli & Corradini (1998) on Pl. 1, Fig. 1a-c and here reillustrated on Pl. 4, fig. 5a-c; IPUM 25834.

Paratypes (figured) – IPUM 25835-25839, 27490-27491.

Locus typicus – Silius I° section, near Silius village, SE Sardinia, Italy.

Stratum typicum – Level SIL I° 5.

Derivatio nominis – From Ichnusa, the ancient Greek name of Sardinia.

Diagnosis (after Serpagli & Corradini, 1998) – The stout Pa element is characterised by fused denticles anterior to the cusp, and by a wide asymmetrical platform bordered by a rim; the inner side of the platform is short and rounded, and bears a simple lateral process. The posterior process is arched downward and gently deflected.

Description – Pa element. The Pa element is usually robust and large in size. The anterior blade is relatively thick, long and straight, and bears nine to fourteen denticles. Anterior to the cusp, two to four denticles are fused together forming a crest (the number of fused
denticles increases in largest specimens). The blade ends anteriorly with three stout, high and discrete denticles followed by one or two very short denticles. In the largest specimens, these small denticles increase in number (up to 5) and decrease in size towards the end of the blade, producing a serrated outline on the anterior margin.

The short posterior blade is arched downward and gently incurved. It bears three to four stout, erect denticles, followed by a small one.

A wide asymmetrical platform is bordered by a rim. On the inner side of the element the platform is short and rounded, and bears a lateral process with one or two denticles aligned perpendicularly to the blade. The outer platform is better developed, has a polygonal outline and bears a complex process with three to eight discrete or closely spaced denticles, sometimes forming a fan-shaped ridge usually more or less parallel to the blade.

The cusp is erect, only slightly larger than adjacent denticles. It is usually connected to the closest denticles on the lateral processes by narrow ridges.

One side of the wide basal cavity is larger than the other one. The cavity extends as a narrow groove to the anterior and posterior ends of the main processes.

Pb, M, Sa, Sb and Sc ELEMENTS. These are apparently indistinguishable from the corresponding elements of _K. v. variabilis_.

Remarks – Pa ELEMENT. The most typical features of _K. v. ichnusae_ (robust blade, posterior process arched downward and gently deflected, wide asymmetrical platform bordered by a rim, short and rounded inner platform with a simple process, fused denticles anteriorly to the cusp, and serrated outline of the anterior margin) co-occur only in adult specimens. In juvenile specimens only some of these features are present. Furthermore, in these specimens, the inner platform may be undentuculated.

The Pa element of _K. v. ichnusae_ differs from that of _K. v. variabilis_, Walliser 1957 mainly by the wider platform, that is bordered by the characteristic rim, by the unbranched inner process and by the occurrence of a crest on the anterior blade.

Few specimens of _K. v. ichnusae_ have a subtriangular basal cavity like that of _K. stauros_ Barrick & Klapper, which, however, has always a simple outer process.

The specimen from New South Wales (Australia) figured by Link & Druce (pl. 3, figs. 11, 12, 15, 16; text-fig, 21) possess most of the features of _K. v. ichnusae_ (including fused denticles anterior to the cusp and fan-shaped ridge of the outer process denticles), except number of denticles on the short inner lateral process.

Range – From the base of the Oz. exc. _hamata_ Zone to the middle part of the _Pol. siluricus_ Zone.

**Studied material** – 81 Pa elements from samples GA 3, FRU B, GCIU 1, GCIU 3, SIL 1° 1, SIL 1° 2, SIL 1° 3, SIL 1° 4, SIL 1° 5, SIL 1° 6, SIL 1° 7, SIL 1° 8, RMC 1, RMC 1B, RMC 1C, SBF 5, GALE BK 8, GALE BK 13, PF 1Q, PF 11B, PF 1H, FTM 1, FTM 2, FTM 2A and SAD 21.

**CONCLUSIONS**

The main results of the studies of the taxonomy and evolution of _Kockeella_ are the following:

1. The number of _Kockeella_ taxa increases, changing from twelve to sixteen;
2. Both _Kockeella variabilis_ and _K. absidata_ have been subdivided into two subspecies;
3. The old problem of the reconstruction of the _K. crassa_ apparatus is finally solved;
4. The reconstruction of the phyletic relations within the genus _Kockeella_ (which largely follows that one of Barrick & Klapper, 1976) shows that three main lineages, all originating from the common ancestor _K. ranuliformis_, are recognisable (Text-fig, 1);
5. _Kockeella patula_ and its possible descendants are still a problem, being difficult to place in our

**EXPLANATION OF PLATE 7**

Figs. 1-7 - *Kockeella variabilis variabilis* Walliser, 1957.
1) IPUM 25855, sample PF 11B (Oz. exc. _hamata_ Zone); upper view (a) and lower view (b) of Pa element; x60;
2) IPUM 25856, sample PF 1Q (Oz. _ploceus_ Zone); upper view (a) and lower view (b) of Pa element; x80;
3) IPUM 25854, sample SIL 1° 3 (Oz. exc. _hamata_ Zone); upper view of Pa element; x80;
4) IPUM 27494/1, sample PF 11B (Oz. exc. _hamata_ Zone); posterior view of Sb element; x55;
5) IPUM 27494/2, sample PF 11B (Oz. exc. _hamata_ Zone); inner-lateral view of Pb element; x55;
6) IPUM 27493/4, sample PF 11B (Oz. exc. _hamata_ Zone); inner-lateral view of Sc element; x60;
7) IPUM 27493/4, sample PF 11B (Oz. exc. _hamata_ Zone); inner-lateral view of M element; x66.

Figs. 8-9 - *Kockeella stauros* Barrick & Klapper, 1976.
8) IPUM 27474, sample GALE BK 18 (_K. crassa_ Zone); upper view (a) and lower view (b) of Pa element; x66;
9) IPUM 27475, sample SF BK 3 (_K. crassa_ Zone); upper view (a) and lower view (b) of Pa element; x66.

Fig. 10 - *Kockeella ranuliformis* (Walliser, 1964). IPUM 25862, sample ARG C (_K. ranuliformis_ Zone); upper view (a) and lateral view (b) of Pa element; x80.
E. SERPAGLI, C. CORRADINI, TAXONOMY AND EVOLUTION OF KOCHELLELLA

Pl. 7
phyletic scheme;
6 - The \( K. \ crassa \) stock up to date does not show a clear link to the main tree and therefore is left to open interpretation;
7 - Two main crises affected the \textit{Kockeella} stock. The first one took place during the late \( Oz. \ s. \ rhenana \) Zone and led to the extinction of \textit{K. ramuliformis}, \textit{K. lattidemata}, \textit{K. corpulentia}, \textit{K. amodeni}, \textit{K. cf. stauros sensu} Bischoff, 1986, \textit{Kockeella} sp. nov. A Klapper & Murphy, 1975 (\textit{sensu} Bischoff, 1986), as well as \( K. \ pattula \). The second crisis occurred just above the Wenlock-Ludlow boundary and affected \textit{K. stauros}, \textit{Kockeella} sp. nov. A Klapper & Murphy 1975, \( K. \ wallisieri \) and \( K. \ crassa \);
8 - The surviving taxa, \( K. \ v. \ variabilis \) and \( K. \ a. \ abisidata \), successfully evolved, producing descendants that reached the late \textit{Pol. silicarius} Zone, when the whole lineage became to the end;
9 - The new species \( K. \ crassa \) and \( K. \ maennikii \) have good stratigraphic value, both being restricted to a short intervals of the Gorstian and of the Ludfordian, respectively.

**AKNOWLEDGEMENTS**

The idea of the present revision arised during a scientific visit by the senior author at the Department of Geology of Lund University. We express our deep gratitude to J. Barrick (Texas Tech University) not only for the revision of the manuscript, but chiefly for the suggestion that “\textit{Oz.} \ crassa \ Walliser joins, as Pb element, \textit{K. circapudatr}a Serpagli & Corradini in the apparatus of \textit{K. crassa}." Discussions and exchange of opinions with L. Jepsson (Lund University) and P. Männik (Tallinn Technical University) greatly improved this paper. O.H. Walliser kindly provided camera lucida drawings and pictures of some specimens from Cellon. Thanks are also due to Mr. Claudio Gentilini for S.E.M. photographs and to Mr. Giancarlo Leonard for graphical support.

Research funded by CNR and MURST grants (40%, 60% and COFIN97, resp. E. Serpagli).

This is a contribution to IGCP project 421 \textit{North Gondwana Mid-Paleozoic Biogeography/Biogeography Pattern in Relation to Crustal Dynamics}.

**APPENDIX 1**

**REMARKS ON SAMPLE LOCATION.**

**Locality abbreviations:**

SE Sardina: GA=Genna Arrela, FRU=Monte Fruccas, GCIT=Genna Ciucicu, SIL I=Silius I, RMC=Riu Murr de Callus, SBF=Sant Basilio Fenigu;

SW Sardina (environ of Fluminimaggiore): GAL=Galemmu, CB III=Corti Baccas 3a, PF=Perd’e Fugo, SF=Sentiero Fluminim [samples SF 7, 8, 9, 12 from Serpagli, 1971];

SW Sardina (other areas): ARG=Argiola, FTM=Funtanamare, SAD=Sant’Antonio di Santadi-Donigala.

For the detailed location of the localities visited during the ECOS VII Sardina field trip refer to the Guide-book (Serpagli, ed., 1998);

Genna Ciucicu (Corradini et al., 1998b, fig. 1.3.1, p. 113), Silius (Serpagli et al., 1998; fig. 1.2.1, p. 105),
Perde Fugo (Ferretti et al., 1998a, fig. 2.2.1, p. 157)
Argiola (Corradini et al., 1998a, fig. 3.3.1, p. 195).

**Remarks on the other localities are as follows:**

Genna Arrela and Monte Fruccas: refer to Corradini & Olivieri (1997, fig. 1);

Riu Murr de Callus: this locality is about 1 Km SE of stop 4.1 of the ECOS VII Sardinia Field trip Guidebook (Ferretti et al., 1998a, fig. 4.1.1, p. 202);

San Basilio Fenigu: this locality is about 1 Km E of stop 1.1 of the ECOS VII Sardinia Field trip Guidebook (Ferretti et al., 1998a, fig. 1.1.1, p. 97);

Galemmu, Sentiero Fluminim Corre: these outcrops are located in the Fluminimaggiore area: refer to the map in Fig. 2.2.1 of the ECOS VII Sardinia Field trip Guidebook (Ferretti et al., 1998a, p. 157);

Funtanamare: village on the south-west coast, 2 Km South of Nebida.
Sant’Antonio Donigala: Sant’Antonio di Santadi-Donigala area, South of Oristano; outcrops close to Case Gasti.

**APPENDIX 2**

**INDEX OF THE ILLUSTRATED SPECIMENS**

With this paper a general synthesis of the whole \textit{Kockeella} of Sardinia is presented. It is, therefore, useful to show again figures of specimens reported on the ECOS VII Sardinia Field-excursion Guide Book (Serpagli, ed., 1998).

**This paper**

<table>
<thead>
<tr>
<th>Pl.</th>
<th>fig.</th>
<th>p.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>157</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>1</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>2</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>4</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>1</td>
</tr>
</tbody>
</table>

**ECOS VII Sardinia Field-excursion guidebook**

<table>
<thead>
<tr>
<th>Pl.</th>
<th>fig.</th>
<th>p.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>17</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>2</td>
<td>18</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>1</td>
</tr>
</tbody>
</table>

**APPENDIX 3**

**DURING THE RESTUDY OF THE SECTIONS Silius I and Genna Ciucicu (both in SE Sardinia) in connection to the preparation of the ECOS VII Field Trip (June 1998), new samples were collected.**

Because the old sample numeration was already complex, we decided to replace it with a new, more simple one. Therefore, a comparative chart of the numbers reported in the preliminary paper (Barca et al., 1995) and the new ones used in the ECOS VII Field trip Guidebook (Serpagli et al., 1998; Corradini et al., 1998b)
is presented below. The new numbers are also marked on the outcrops.

<table>
<thead>
<tr>
<th>Silius I (^{\circ}) section</th>
<th>Genna Ciuciu section</th>
</tr>
</thead>
<tbody>
<tr>
<td>old</td>
<td>new</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>2A</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>3A</td>
<td>5</td>
</tr>
<tr>
<td>3B</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>4A</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>6A</td>
<td>12</td>
</tr>
<tr>
<td>6B</td>
<td>14</td>
</tr>
<tr>
<td>6C</td>
<td>15</td>
</tr>
<tr>
<td>7</td>
<td>16</td>
</tr>
<tr>
<td>7A</td>
<td>17</td>
</tr>
<tr>
<td>7B</td>
<td>18</td>
</tr>
<tr>
<td>8</td>
<td>19</td>
</tr>
<tr>
<td>8X</td>
<td>20</td>
</tr>
<tr>
<td>8A</td>
<td>21</td>
</tr>
<tr>
<td>8Y</td>
<td>22</td>
</tr>
<tr>
<td>8B</td>
<td>23</td>
</tr>
<tr>
<td>9</td>
<td>24</td>
</tr>
<tr>
<td>10</td>
<td>26</td>
</tr>
<tr>
<td>10A</td>
<td>27</td>
</tr>
<tr>
<td>27</td>
<td>11B</td>
</tr>
<tr>
<td>11</td>
<td>11C</td>
</tr>
<tr>
<td>30</td>
<td>12</td>
</tr>
<tr>
<td>11A</td>
<td>31</td>
</tr>
<tr>
<td>12A</td>
<td>32</td>
</tr>
<tr>
<td>12B</td>
<td>33</td>
</tr>
<tr>
<td>13</td>
<td>34</td>
</tr>
<tr>
<td>14</td>
<td>35</td>
</tr>
<tr>
<td>36</td>
<td>15</td>
</tr>
<tr>
<td>37</td>
<td>15A</td>
</tr>
<tr>
<td>38</td>
<td>16</td>
</tr>
<tr>
<td>39</td>
<td>19</td>
</tr>
<tr>
<td>50</td>
<td>20</td>
</tr>
</tbody>
</table>

REFERENCES


SERPAGLI, E., 1967, Prima segnalazione di Conodonti nel Siluriano della Sardegna e relative osservazioni stratigrafiche: Accademia Nazionale dei Lincei, Rendiconti della Classe di Scienze Fisiche, Matematiche e Naturali, 42 (6), ser 8: 856-858.


(Manuscript received January 26, 1999 accepted July 19, 1999)

Enrico SERPAGLI
Carlo CORRADINI
Dipartimento di Scienze della Terra (Palaeontologia)
Università di Modena e Reggio Emilia
Via Università 1, I-41100 Modena, Italia
E-mail: serpagli@unimo.it; corre@unimo.it