Debate on skeletal elements of the Triassic conodont *Cornudina* Hirschmann

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ABSTRACT:

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The long-ranging Early to Middle Triassic coniform conodont form-genus *Cornudina* Hirschmann occurs abundantly in the Anisian of NW Turkey, Northern Tethys. Although suggested to represent the P1 element of an apparatus of the Order Ozarkodinida Dzik, questions concerning the apparatus of *Cornudina* remain. A description of the probable phylogenetic trends in the P1 elements of *Cornudina* is attempted and the role of the form-genera *Ketinella* Gedik and *Kamuellerella* Gedik, as the alternative ramiform skeletal elements in the *Cornudina* multi-element apparatus, is investigated. The newly described, *Gedikella quadrata* gen. nov., sp. nov., is an S element, *Kamuellerella rectangularis* sp. nov., is either an S3 or an S4 element, and *Ketinella goermueshi* sp. nov., is an M element.

Key words: *Cornudina*; Apparatus; Multielement; Conodont; Triassic; Kocaeli Peninsula.

INTRODUCTION

In conodont systematics, form taxonomy has long prevailed until the discovery of natural assemblages of conodont apparatuses and the subsequent establishment of multielement taxonomy. Nowadays, it has become common to use the abbreviated positions P1, P2, M, S0, S1, S2, S3 and S4 instead of naming the original form-species of each skeletal component (Purnell *et al.* 2000). Since the composition of the skeletal apparatus has significance for determination of the family or subfamily to which a conodont genus belongs, it is of prime importance to consider the form-species at the origin of the skeletal elements. Many such elements belong to genera that have little changed since their Paleozoic ancestors and only a few species have been erected for

Triassic forms, such as *Cratognathodus*, *Ketinella* and *Kamuellerella* that also designate skeletal apparatus-elements.

The form-genus *Cornudina* Hirschmann, a coniform P1 which first appeared in the Smithian, flourished during the Spathian and numerically decreased during the Middle Triassic (Text-fig. 1).

Although Koike (1996) and Orchard (2005) attempted to integrate these conical elements within a multi-element apparatus, proposing ramiform elements as skeletal parts, such reconstructions remained insignificant. Furthermore, no phylogenetic trends in *Cornudina* have been proposed nor discussed in detail.

A few authors have addressed these small conodont forms (Kozur and Mostler 1970, 1971a, b, 1972; Gedik 1975; Koike 1996, 1998, 1999).
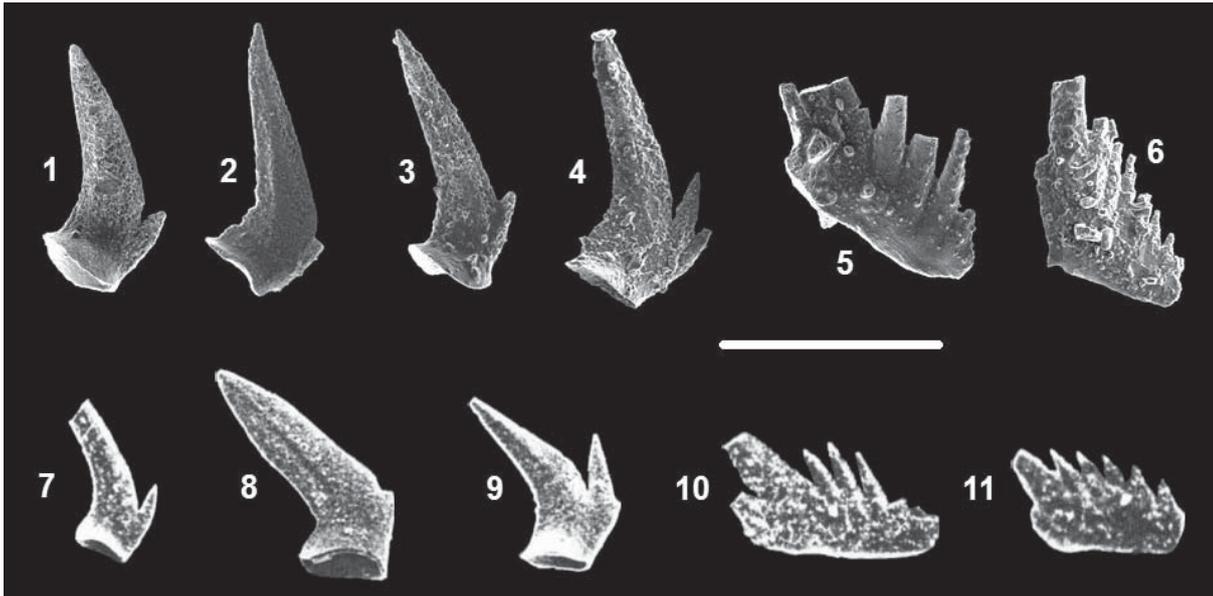
Text-fig. 1. Tethyan cornudinid elements: 1-4, 7-9 – *Cornudina oezdemirae* Gedik, 1975; 5-6, 10-11 – *Cornudina* ? *latidentata* Kozur and Mostler, 1970. 7-11 – specimens of Gedik (1975) and others from Kılıç (2004). Scale bar 150 μm

MATERIAL AND METHODS

The section of Gedik (1975; p. 108, fig. 5, section 3) was sampled at ~25 cm intervals in order to achieve a high-resolution stratigraphic dataset for precise determination of conodonts. Conodont samples (1–3 kg per layer) were dissolved in acetic acid (8–12%), the insoluble residues were washed and fractioned by sieving (2.00 mm and 73 μm). Conodonts and insoluble residues are archived at the Department of Geological Engineering, University of Balıkesir.

STRATIGRAPHICAL FRAMEWORK

We adhere to the nomenclature of the Stratigraphic Committee of Turkey (Tüysüz *et al.* 2004) as a summary because the aim of present paper isn't a comprehensive description and interpretation of the Kocaeli Triassic. The Triassic sequence in the Kocaeli Peninsula is composed of six formations (Text-fig. 2). While the lowest Kapaklı Formation is still terrestrial, the others are transgressive as witnessed by environmental features. The sequence and environmental features of the formations exhibit similar appearances all over the peninsula. In the vicinity of Tepecik (Tepeköy) region, the Tepeköy Formation overlies the Ballıkaya Formation, well developed in the southern and especially middle parts of the Kocaeli Peninsula where its typical features can be seen. Only the samples taken from south of Gebze, which are considered taxonomically important to this study are listed and the other fossil data will be presented later.

SYSTEMATIC PALAEONTOLOGY

This part was written by first author and all figured specimens are kept in the Department of Geology, Faculty of Engineering and Architecture, Balıkesir University.

Order Ozarkodinida Dzik, 1976
Superfamily Gondolelloidea (Lindstroem, 1970)
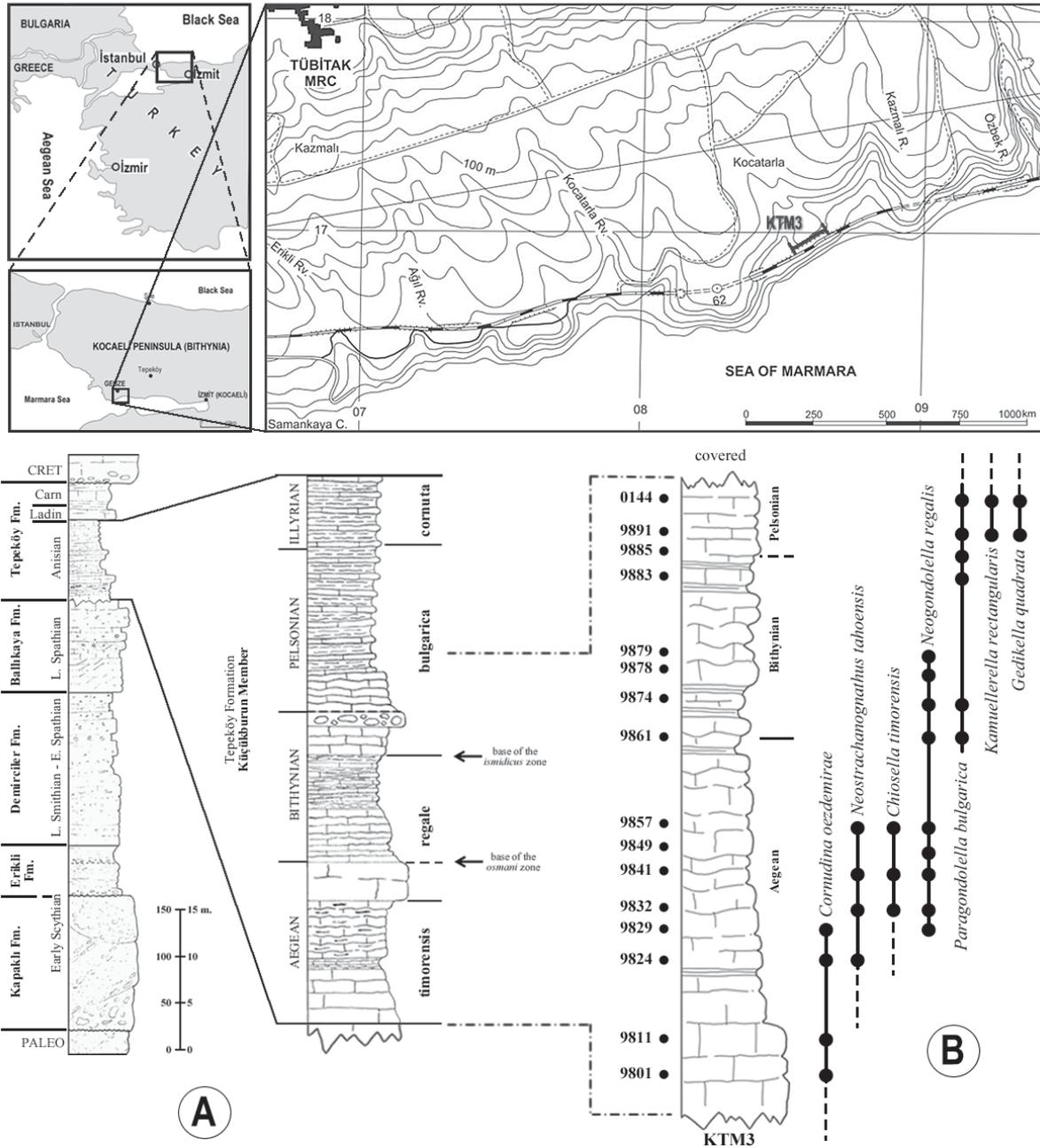Family Gondolellidae (Lindstroem, 1970)
Genus *Cornudina* Hirschmann, 1959

TYPE SPECIES: *Ozarkodina breviramulis* Tatge, 1956

Cornudina oezdemirae Gedik, 1975
(Text-figs 1.1–1.4, 1.7–1.9)

1968. *Cornudina breviramulis breviramulis* Tatge; Kozur, pl. 3, fig. 29.
1970. *Cornudina* ? *latidentata* sp. nov., Kozur and Mostler, pl. 1, fig. 21.

Text-fig. 2. Location map and locations of measured stratigraphic section (South of Gebze, Marmara Sea coastline). Stratigraphic Columnar Section (after Assereto 1974; Gedik 1975; Kılıç 2004) of the Kocaeli Triassic (Text-fig. 1A) and measured columnar section of Tepeköy formation (Text-fig. 1B)

1975. *Cornudina oezdemirae* sp. nov., Gedik, pl. 7, figs 15, 24 (holotype), 29.

1982. *Cornudina breviramulis minor* Kozur and Mostler; Koike, pl. 7, fig. 4.

1996. *Cornudina igoi* sp. nov.; Koike, figs 4.1–4.20.

2005. *Cornudina igoi* Koike, 1996; Orchard, text-fig. 1, Pa element.

DESCRIPTION: The unit is composed of a long cusp and an anterior process. The cusp is inclined posteriorly at 40–50 degrees. The length of the basal margin of the unit ranges from 150 μm to 220 μm and the cusp ranges in length from 240 μm to 340 μm (Koike 1996). The anterior process has one to four denticles. In some specimens one minute denticle is present

just behind the cusp. The anterior denticles increase in length and their inclination augments posteriorly; anterior denticles are fused or separated. The basal cavity is laterally expanded and elongated in function of the number of the anterior denticles, showing a drop shape in cross-section.

REMARK: *Cornudina oezdemirae* differs from *C. breviramulis* in having no distinctive denticle behind the cusp.

RANGE: The unit ranges from the Early Triassic (Taho Formation, Japan; Koike 1996), to the Middle Triassic (Kocaeli Peninsula; Gedik 1975).

Genus *Kamuellerella* Gedik, 1975

TYPE SPECIES: *Kamuellerella gebzeensis* Gedik, 1975

ARRAY: *Kamuellerella* (*Kamuellerella*) *gebzeensis* Gedik, *K.* (*K.*) *seymeni* Gedik, *K.* (*K.*) *subsymmetrica* Gedik, *K.* (*K.*) *yurtseveri* Gedik, *K.* (*Neobelodina*) *brevibasalis* Gedik.

Kamuellerella rectangularis sp. nov.
(Text-figs 3.7–3.8)

ETYMOLOGY: *Kamuellerella* form with height to length ratio, making it fitting a rectangle.

HOLOTYPE: The specimen from Text-fig. 3.8.

TYPE LOCALITY: KTM3 measured section located between the Ortadere and Kurtdere, SE Gebze (Kocaeli, Turkey).

MATERIAL: 42 specimens.

DIAGNOSIS: Unit narrow, with denticles curved toward posterior; main cusp located in terminal end and straight; in some specimens denticles increase posteriorly.

DESCRIPTION: The flat lying main cusp of *Kamuellerella rectangularis* sp. nov. is very straight in the posterior end (Text-fig. 3.8). The anteriormost denticle is smaller than the previous two-three denticles. Other anterior denticles are bigger than the next six-seven denticles. The holotype corresponds to the S1 element.

REMARKS: *Kamuellerella rectangularis* sp. nov. is

transitional between *Kamuellerella seymeni* Gedik, 1975 and *Gedikella quadrata* gen. nov., sp. nov.

RANGE: Upper Anisian (Pelsonian–Illyrian?) of the Kocaeli Peninsula, NW Turkey.

Genus *Gedikella* gen. nov.
(Text-fig. 3.9–13)

TYPE SPECIES: *Gedikella quadrata* sp. nov.

ETYMOLOGY: In honour of Dr. İsmet Gedik, Karadeniz Technical University, Turkey.

MATERIAL: 367 specimens.

DIAGNOSIS: Unit straight, very small, short and narrow; 9–11 denticles inclined posteriorly; basal groove expanded sometimes under main cusp. Height-length ratio nearly equal.

RANGE: Anisian (Pelsonian–Illyrian?) of the Kocaeli Peninsula, NW Turkey.

Gedikella quadrata sp. nov
(Text-figs 3.9–3.13)

ETYMOLOGY: After the quadrate unit outline (height and length relations).

HOLOTYPE: The specimen in Text-fig. 3.9.

TYPE LOCALITY: KTM3 measured section located between the Ortadere and Kurtdere, SE Gebze (Kocaeli, Turkey).

MATERIAL: 156 specimens.

DIAGNOSIS: As for the genus.

DESCRIPTION: Some specimens have one or two minute denticles behind the main cusp (Text-figs 3.11, 3.13) or inward inclined denticles (Text-fig. 3.12). One smaller specimen shows denticles curved backward (Text-fig. 3.10). The holotype corresponds to S1 element.

REMARKS: *Gedikella quadrata* gen. nov. sp. nov. differs from *Kamuellerella seymeni* by its flat lying main cusp in the continuation of the rather smooth basal part of the unit. The main cusp of *K. rectangularis* sp. nov. (Text-fig. 3.8) is very straight in the
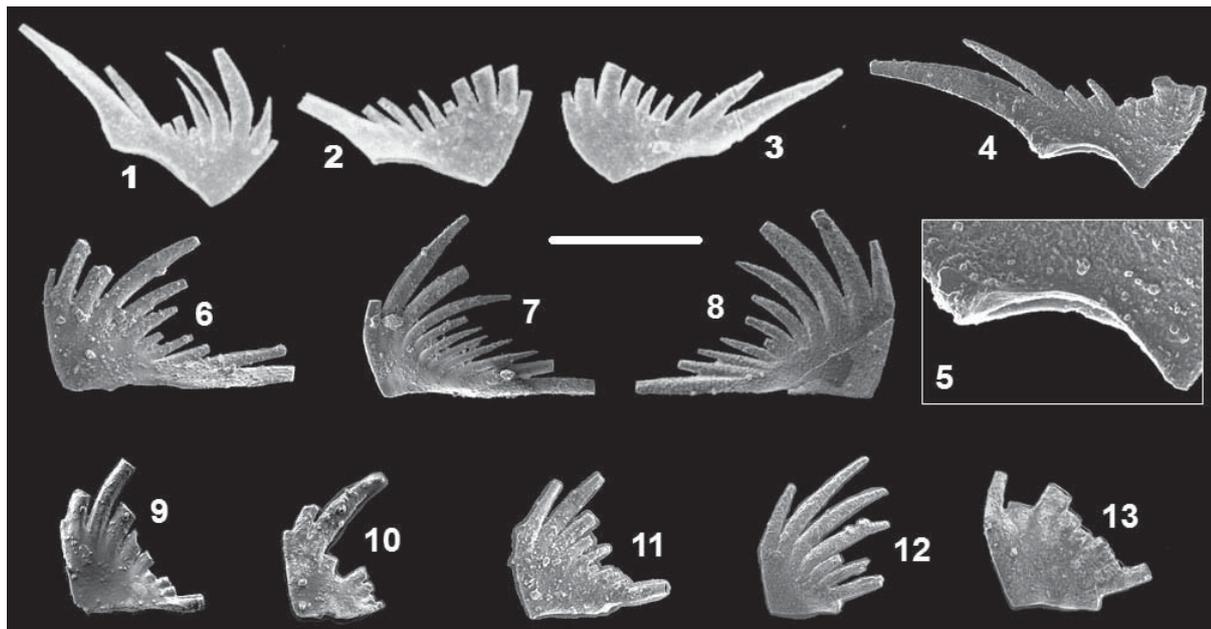
Text-fig. 3. Form-species of *Kamuellerella seymeni* Gedik, 1975, *Kamuellerella rectangularis* sp. nov. and *Gedikella quadrata* gen. nov. sp. nov.; **1-6** – *Kamuellerella seymeni* Gedik, 1975; 6 – bended form; 7 – transitional form between *K. seymeni* and *K. rectangularis* sp. nov.; **8** – *Kamuellerella rectangularis* sp. nov.; **9-13** – *Gedikella quadrata* gen. nov. sp. nov.; 9 –holotype, 10-13 – paratypes. Anisian. 1-3 – specimens of Gedik (1975) and others from Kılıç (2004). Scale bar 150 μm

posterior end. This form-species is assumed to be coeval with the hindeodelliform Sc1 (S3) and Sc2 (S4) elements of the octomembrate Neogondolellid apparatuses of Orchard and Rieber (1999).

RANGE: Anisian (Pelsonian–Illyrian?) of the Kocaeli Peninsula, NW Turkey.

Genus *Ketinella* Gedik, 1975

TYPE SPECIES: *Ketinella maxicavata* Gedik, 1975

ARRAY: *Ketinella maxicavata* Gedik, *K. langeri* Gedik

Ketinella goermueshi sp. nov.
(Text-figs 4.16–4.23)

ETYMOLOGY: In honour of Dr. Muhittin Görmüş, Ankara University, Turkey.

HOLOTYPE: The specimen on Text-figs 4.18 and 4.18a.

TYPE LOCALITY: KTM3 measured section located between Ortadere and Kurtdere, SE Gebze (Kocaeli, Turkey).

MATERIAL: 44 specimens.

DIAGNOSIS: Long, large and sharp pointed main cusp and 3–4 bilaterally decreasing denticles; sometimes one germinal denticle; quite small basal part and rather narrow basal cavity, as compared to other *Ketinella* species.

DESCRIPTION: This is the elongate element with 3–4 moderately fused denticles increasing toward the main one. The aboral margin is straight. The lower surface is marked by a narrow longitudinal groove.

REMARKS: This species is very similar to *C. gondolelloides* (Bender, 1968) which is considered to be the oldest species of *Chiosella* according to present data, and is distinguished from the latter by its relative length and the development of lateral median ridges. The development of lateral median ridges is one of the key characters defining this species.

RANGE: Anisian (Pelsonian–Illyrian?) of Kocaeli Peninsula, NW Turkey.
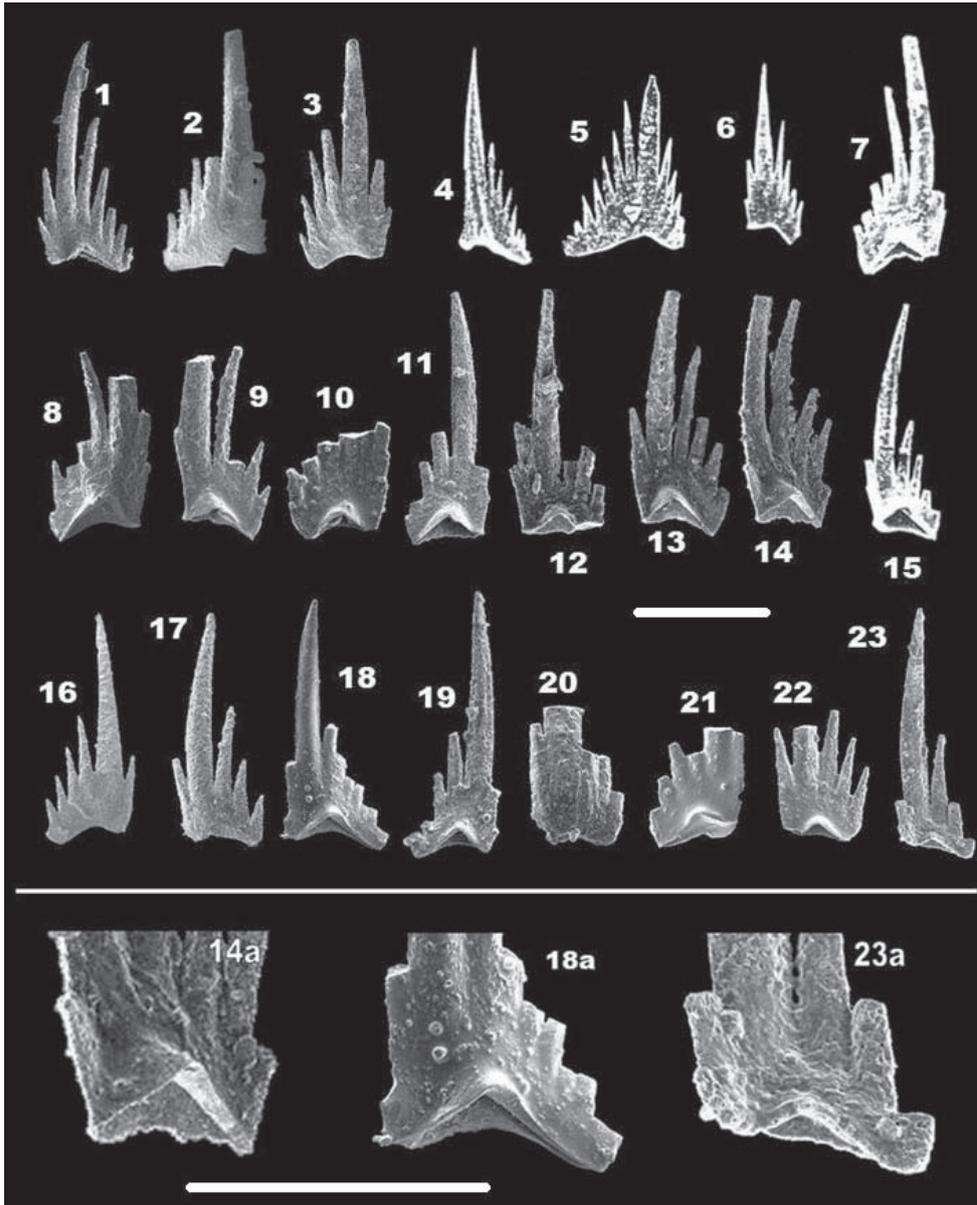
Text-fig. 4. Form-species of *Ketinella* Gedik, 1975. **1-5** – *K. langeri* Gedik, 1975; **6-15** – *K. maxicavata* Gedik, 1975; **16-23** – *K. goermueshi* sp. nov.; **18, 18a** – holotype, 4-7, and 15 are from Gedik (1975), others from Kılıç (2004); Anisian. Scale bar 75 μm

RANGE AND EVOLUTIONARY TRENDS OF *CORNUDINA* HIRSCHMANN

Hirschmann's (1959) original diagnosis of the form-genus *Cornudina* is that of the generotype *Ozarkodina breviramulis* Tatge (1956; p. 139, pl. 5, fig. 12a, b), from the Lower Muschelkalk Kalkwerk Quarry, Trubenhausen, Germany. Hirschmann's holotype of *Cornudina breviramulis* (1959, p. 44) appears to be a P2, a small angulate element with a large and prominent medial cusp and very short upturned processes, while the P1 element has a long cusp, twice the length of the adjacent denticle, an anterior process, and a broadly excavated basal cavity. The length of the anterior process shows specific changes. The basal cavity is clearly elongated in some species. Several small-size ramiform elements with a relatively long cusp, short antero-posterior processes and few denticles, ranging in age from Olenekian to Upper Triassic in various places

of the Tethyan region have also been referred to the form-genus *Cornudina*. The first Muschelkalk collections described by Tatge (1956) do not include a P1 element as do the ones described in Koike (1996), Orchard (2005), and herein.

In several parts of the Tethyan region *Cornudina* is associated with several form-genera, such as *Prioniodina*, *Chirodella*, *Hindeodella*, *Neohindeodella*, and *Diplododella*. While *Chirodella* (*Metalonchodina triquetra*) could be an S1 element, no *Chirodella sensu stricto* occurs in the present collections, nor apparently in those from Japan and China.

The form-species *Cornudina breviramulis* includes (after Kozur and Mostler 1972): *C. breviramulis breviramulis* (Tatge), *C. breviramulis minor* Kozur, *C.? latidentata* Kozur, *C. multidentata* Kozur and Mostler, *C. spassovi* (Stefanov), *C. ancoraeformis* Kozur and Mostler, *C. tortilis* Kozur and Mostler, *C. unidentata* Kozur and Mostler, and *C. pandodentata* Kozur and Mostler. *Cornudina hirschmanni* Pomesano-Cherchi, *C. oezdemirae* Gedik and *C. igoi* Koike can be added to this list.

For reasons of priority, *Cornudina oezdemirae* Gedik (1975), with one anterior denticle, may include *C. igoi* Koike (1996), although the anterior process of the latter has up to three discrete denticles. Koike's (2006) comment about the up to 4 discrete denticles instead of one to three, modifies the multi-element description of *Cornudina* in Orchard (2005, text-fig. 1A). *Cornudina oezdemirae* Gedik shows an evolutionary trend of decreasing total length of the anterior processes and number of discrete denticles, ranging from three to one minute denticle just behind the cusp.

Different stages in the development of *Cornudina* have been interpreted as growth stages, but, may represent evolutionary steps (Text-fig. 5). This may be the case with Orchard's (2007) differentiation between Olenekian and Middle Triassic cornudinids, the distinction based possibly on the increasing number of anterior denticles.

For Orchard (2005), the genera *Spathicuspus* and *Cornudina* constitute the subfamily Cornudininae

Orchard (2005). The Spathian to Anisian genus *Spathicuspus* (formerly *Neospathodus spathi* Sweet), has a prominent cusp and is believed to be the ancestor of the genus *Cornudina*, which appeared near the Early ⁄ Middle Triassic boundary through overall shortening of the P1 element, enlargement of the cusp and process reduction in the M element.

However, for Kozur (2004) *Cornudina* evolved from the late Permian *Merrillina postdivergens*, and for Orchard (2005) the origin of Cornudininae may derive from *Neospathodus chii*, which has a pronounced terminal cusp.

DISCUSSIONS

The Early Triassic genera *Aduncodina* Ding and *Neostrachanognathus* Koike are characterized by the presence of coniform elements in their apparatus (Ding 1983; Kozur and Mock 1991; Koike 1998). Koike (1998) proposed a multielement reconstruction for each genus. Agematsu *et al.* (2008) proposed an incomplete apparatus of *Neostrachanognathus*, consisting of *N. tahoensis* Koike and of a *Neostrachanognathus* sp.. Elements corresponding to the S0 and M positions, as occur in typical 15-element ozarkodinid apparatuses, are not found in the natural assemblage of *N. tahoensis*. Superposed ramiform elements in S positions resemble each other in shape and the S1 to S4 elements cannot be differentiated, due to poor preservation of the natural assemblages, and therefore the term S is used for all elements in all S positions (Agematsu *et al.* 2008).

Neostrachanognathus has a suite of ramiform S elements (e.g. *Oncodella obuti* Buryi) that for Orchard (2005, p. 76) strongly resembles those of Cornudininae (Orchard 2005), but he didn't integrate the genus into the subfamily. Also, extremely thin, blade-like elements (cf. Carnian *Prioniodella* (= *Neohindeodella*?) *dropla* Spasov and Ganev, Text-fig. 6.5; or else *Neohindeodella triassica*, Text-fig. 6.2) with a gross-morphology similar to Cornudininae

oezdemirae   igoi   ? multi- / latidentata
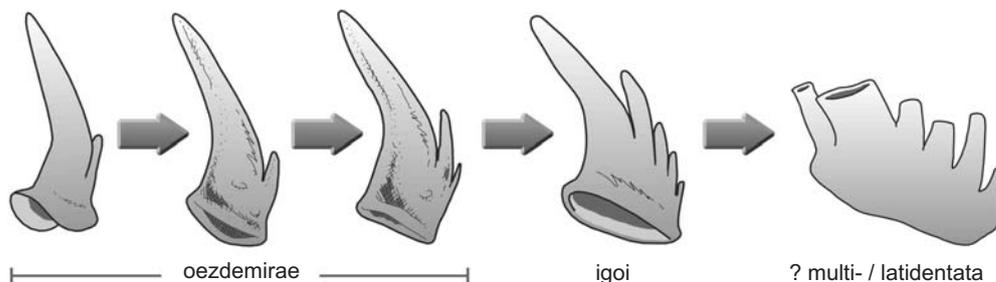
Text-fig. 5. The growth of the basal cavity is proportionately to the progress of the anterior process in *Cornudina*

S elements also appear in the latest Spathian and may derive from *Neostrachanognathus.*

THE *CORNUDINA* SUPRAGENERIC TAXONOMY

The subfamily Cornudininae was defined by Orchard (2005) with a 15-element apparatus including typically short, segminate or rarely segminiplanate P1 elements with a prominent cusp; angulate P2 elements with short subequal processes and prominent cusps; breviform digyrate M elements with two straight, denticulated, relatively short, and downwardly directed processes; modified alate S0 element with two antero-lateral processes; breviform digyrate S1 elements; small digyrate S2 elements with some denticulation on two antero-lateral processes; and bipennate S3–S4 elements with variably inturned and downturned anterior processes. The denticulated anterior process are composed of long arcuate denticles while the posterior processes bear denticles that increase in size distally.

Nevertheless, some objections can be made to this model. Firstly, the lack of statistical data and the absence of the natural assemblage render the understanding of this reconstruction very difficult. Secondly, Orchard's M element would correspond to a Ketinellid form-type, and the element S to a Kamuellerellid form-type; despite the fact that *Ketinella* occurs in different parts of the world (Turkey, Israel, Japan, China), both *Ketinella* and *Kamuellerella* are rarely found with *Cornudina*. We consequently cannot endorse this multielement-reconstruction as well as the establishment of the subfamily Cornudininae.

In this context the question of the apparatus arises as the accepted symbols of P1, P2, M, S0, S1, S2, S3, S4, use form-species that are mostly first described in the Paleozoic. But since there exists variability among most of these, something that has called for the description of additional taxa, the question is what to do with these variants? Some can be related to different families (like between Gondolellidae and Gladigondolellidae), but others may just be similar evolution within the elements of the apparatus in the course of the Triassic. And here comes *Ketinella* that has been recognized by Benjamini and Chepstow (1986) in an apparatus of a very primitive taxon of the family Gondolellidae. The value of such additional form-species is that they signal the morphological differences that otherwise get lost when using letter – symbols (F. Hirsch, personal communication).

SIMILAR MORPHOLOGY

Thought there is great morphologic similarity between genera such as *Cornudina* and *Zieglericonus*, there exists no phylogenetic lineage that links these taxa. Their homeomorphy is not the result of anagenesis but only of similar functional structures, reduced to their minimal expression. The phenomenon is characteristic atavism, the reappearance of ancestral forms. Anagenetic lineages may be paced by atavistic reversals, as it is the case for the genera *Neospathodus* and *Misikella*. No such relation is known for the genus *Cornudina* as well as for *Zieglericonus*.

THE *CORNUDINA* MULTI-ELEMENT AND ITS SKELETAL COMPOSITIONS

Two different models for the *Cornudina* apparatus have been proposed; one in which the apparatus was composed of one or two morphological types of elements (Koike 1996), and the other one following the typical octomembrate apparatus of Triassic Gondolelloidea (Orchard 2005).

### Uni-membrate or bimembrate *Cornudina* apparatus

Koike (1996) recognized *Cornudina breviramulis* (Tatge) as a bimembrate apparatus encompassing P1 and P2 elements, and *C. igoi* Koike as a unimembrate apparatus.

Koike's (1996) P1 element in the skeletal apparatus of *C. breviramulis* refers to the form species *C. breviramulis* by Tatge (1956) from the upper Lower and the Upper Muschelkalk, of Anisian to Ladinian age of Germany. His P2 element refers to the form species *C. tortilis* Kozur and Mostler (1970), from the Lower Muschelkalk of Germany. The skeletal apparatus of *C.breviramulis* (Tatge) ranges from the Smithian through Carnian (Koike 1996).

The unimembrate skeletal apparatus of *C. igoi* Koike consists only of the P1 element of form species *C. igoi* Koike (1996) from the Spathian interval of the Taho Formation (SW Japan) and from the Lower Anisian interval of the Kodiang Formation in West Malaysia (Koike 1982).

The Multi-element of *Cornudina*

Sweet (in Clark *et al.* 1981, p. W155) placed *Cornudina* with *Chirodella* in the multielement of
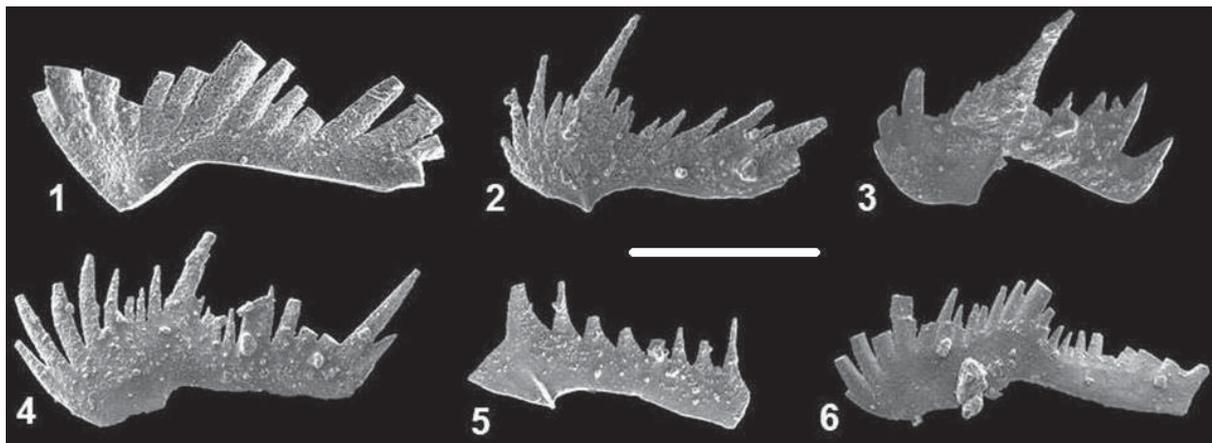
Text-fig. 6. Some ramiform elements (Kılıç 2004) proposed for multielement *Cornudina* Hirschmann, 1959. 1 – *Hindeodella suevica* (Tatge, 1956); 2-3 – *Neohindeodella triassica* (Müller, 1956); 4 – *N. Aequiramosa* Kozur and Mostler, 1970; 5 – *N. Dropla* Spasov and Ganev, 1960; 6 – *Veghella delicatula* Budurov, 1960. Scale bar: 150 μm

Chirodella, but Koike (1996) and Orchard (2005) regarded these two genera as unrelated.

Orchard (2005) objected to Koike's (1996) bi-elemental *Cornudina* apparatus as being incomplete and proposed an octomembrate apparatus (see description above) from material originated from the Tethyan, Anisian Upper Guangdao section, Nanpanjiang Basin, South China. Unfortunately, Orchard did not specify if the elements come from monofaunal samples.

THE ROLE OF *KETINELLA*, *KAMUELLERELLA* AND *NEOSTRACHANOGNATHUS* AS SKELETAL ELEMENTS IN A MULTI-ELEMENT APPARATUS

All species from the Tethyan Anisian of the Kocaeli Peninsula of NW Turkey, that were classified in the genera *Ketinella* and *Kamuellerella* by Gedik (1975), correspond to M and S elements. A cornudinid M element in Orchard (2005), characterized by two short straight processes, is identical with that in *Ketinella* (Gedik 1975; pl. 5, figs 9–11, 14, 18).

Further comparison of elements in Cornudininae with those of other multi-elements, as the P2 element (Orchard 2005, text-fig. 1B), corresponds, in our opinion, to a "juvenile"

cratognathid form. While a cratognathid element makes sense as a P2 element, this designation makes the element definitely a part of a gladigondolellid apparatus, and is incompatible with gondolellid elements forming a multi-element together.

Concerning the S elements, the use of the form species *Kamuellerella gebzeensis* (Gedik, 1975; pl.

8, fig. 2) to identify the S3 element (in Orchard 2005; text-fig. 1F) would confer a more precise definition. As S0, the bipennate *Veghella delicatula* Budurov, 1960 (Text-fig. 6.6) or *Prioniodina latidentata* Tatge, 1956 are proposable alternatives. With its anterolateral processes far anterior of the cusp, this form can be compared to a Kamuellerellid form species. The S2 element of Orchard (2005; text-fig. 1D) may be *Hindeodella suevica* Tatge, 1956 (Text-fig. 6.1) or, as suggested here, *Kamuellerella yurtseveri* (Gedik, 1975; pl. 8, fig. 9). Alternatively, as an S2 element, *Neohindeodella aequiramosa* Kozur and Mostler, 1970 is preferred: (Text-figs 6.3, 6.4). Furthermore, *K. yurtseveri* Gedik, 1975 (Text-figs 6.1–6.2) differs only by the position of the main cusp from *H. suevica*. Is this feature sufficient for it to be chosen as a S2 element? This form expands anteriorly and has a terminal main cusp [see also *K. seymeni* (Gedik, 1975; pl. 8, figs 3, 7, 8)] (Text-figs 3.1–3.6). Careful examination of kamuellerellids reveals clearly that some *K. gebzeensis* forms are more applicable because of their digyrate (enantiognathiform) shape (Text-fig. 7).

Arcuate S3–S4 elements become different with two features: the position and the angle of the main cusp and the shape of the arcuate basal part. *K. gebzeensis* Gedik (1975; pl. 8, figs 1, 2, 4) has a long posterior process and generally its basal part is wavy-looking (Text-fig. 8). Despite of this form, *K. subsymmetrica* Gedik (1975; pl. 8, figs. 5, 6, 10) has no wavy-looking basal part and a long posterior process (Text-figs 7.3–7.8); whereas the angle of the main cusp of *K. gebzeensis* has a range of 20–500,
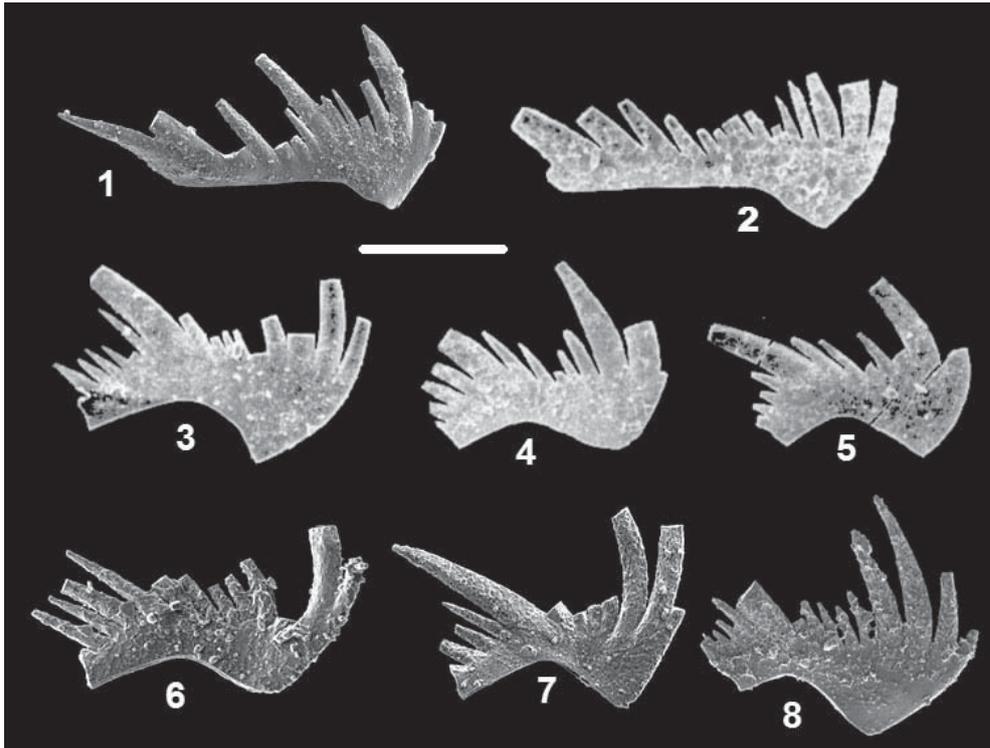
Text-fig. 7. Form-species of *Kamuellerella subsymmetrica* Gedik, 1975 and *K. yurtseveri* Gedik, 1975. **1-2** – *K. subsymmetrica* Gedik, 1975; **3-8** – are *K. yurtseveri* Gedik, 1975. 2-5 are specimens of Gedik (1975), others from Kılıç (2004); Anisian. Scale bar 150 μm
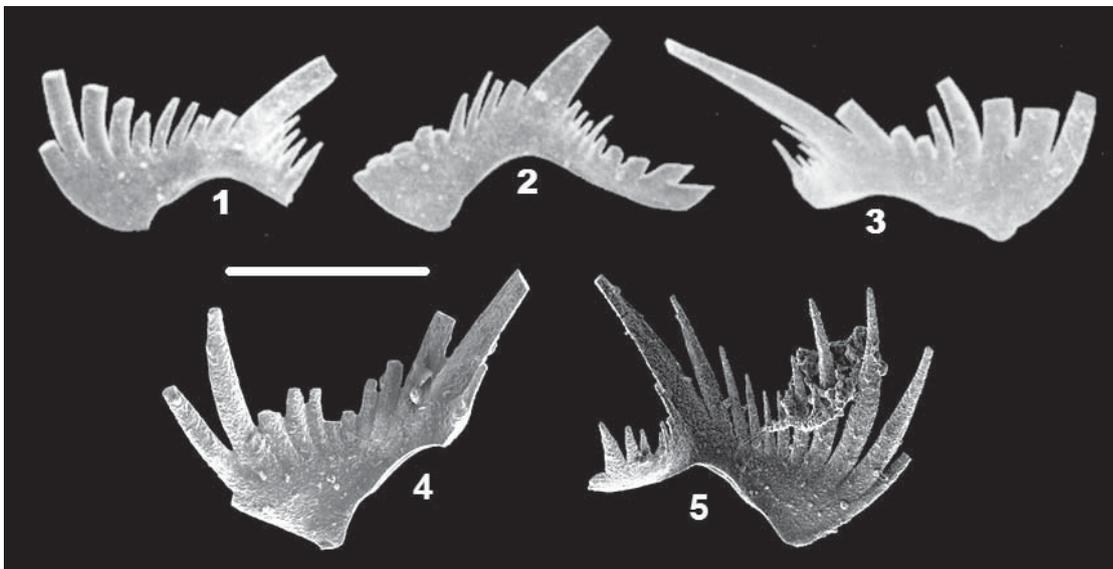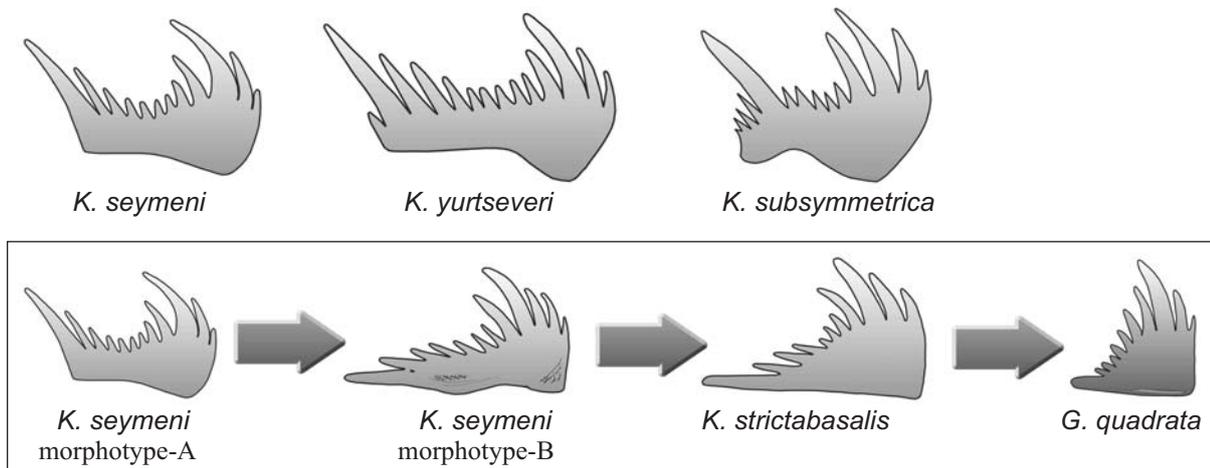

Text-fig. 8. Form-species of *Kamuellerella gebzeensis* Gedik, 1975. **1-3** – specimens of Gedik (1975); **4-5** – from Kılıç (2004); Anisian. Scale bar: 150 μm

the angle of the main cusp of *K. subsymmetrica* has a range of 30–400.

In the form species *K. seymeni* the position of the main cusp varies substantially, located in the terminal or in the anterior part. The main cusp is sometimes curved (Text-fig. 3.4) and the denticles of the

Text-fig. 9. Evolutional relationship between the Kamuellerellids (*Kamuellerella subsymmetrica* Gedik, 1975, *K. yurtseveri* Gedik, 1975, *K. seymeni* Gedik, 1975, *K. rectangularis* sp. nov.) and *Gedikella quadrata* gen.nov. sp. nov.
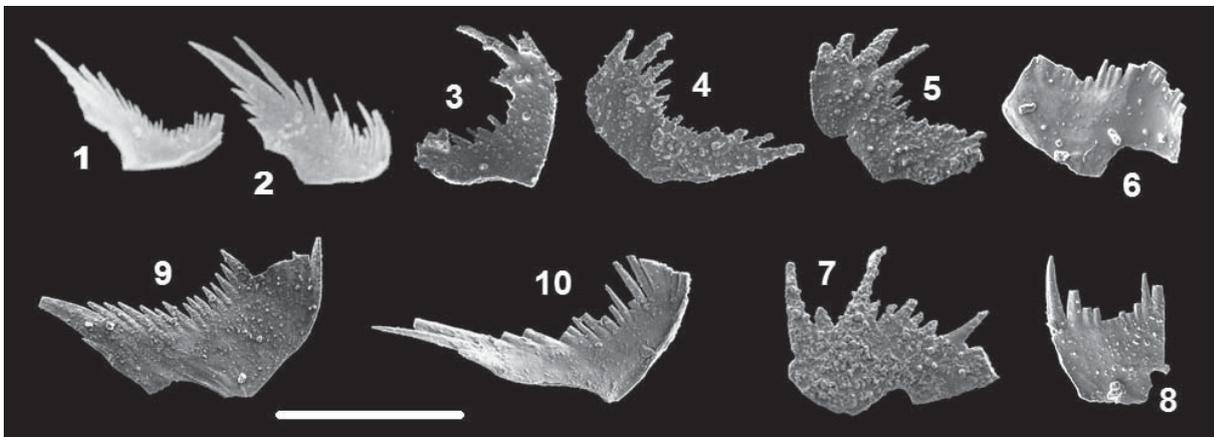
Text-fig. 10. Form-species of *Kamuellerella* (*Neobelodina*) *brevibasalis* Gedik and some new Kamuellerellids. **1-4** – *K.* (*Neobelodina*) *brevibasalis*; **5-10** – New forms; 1-2 specimens of Gedik (1975); all others from Kılıç (2004), Anisian. Scale bar 100 μm

anterior part bent to the right (Text-figs 3.4, 3.6). In some forms, the basal cavity expands gradually (Text-fig. 3.5). The position of the main cusp increasingly diverges in the younger forms of *Kamuellerella*. In some specimens of this form-species the main cusp is in the terminal end position and the entire unit is bent. The original shape of this form can be seen in Text-figs 3.6, 3.7. The forms that are smaller than young kamuellerellids (Text-figs 3.9–3.13), having 8 to 10 denticles and being quite short, belong to a new form-genus showing a gradual evolution over a very short interval. Their basal cavities are located in the middle part of the unit. In the holotype of isosceles right triangle shape (Text-fig. 3.9), the position of the main cusp is still in the terminal end. The next forms have one or two minute denticles backwards of the

main cusp (Text-figs 3.11, 3.13), whereas the denticles of younger forms are curved backward (Text-fig. 3.12), and the youngest forms are quite smaller. The position of the main cusp corresponds to the larger part of the basal cavity. The denticles of some of these forms are curved completely inwardly. The evolutionary relationships of these forms are seen in Text-fig. 8.

Form species *K.* (*Neobelodina*) *brevibasalis* Gedik, 1975 is the smallest kamuellerellid and has a quite different delicate structure (Text-figs 10a, b and 10.1, 10.2). In the present fauna some related forms are new (Text-figs 10.3–10.9).

Concerning the *Neostrachanognathus* multielement, Agematsu *et al.* (2008) reported two P3 elements that vary in shape from digyrate coniform to digyrate, suggesting that this difference reflects the

variability of the P3 elements within the apparatus of the living conodont. Although the relationship is not supported by the entire multielement data, this morphological similarity of *Ketinella* and the P3 element in the multi-element of *Neostrachanognathus* must be considered.

The form species in Text-fig. 3 and 9 are problematical for multielement reconstruction.

CONCLUSIONS

(1) Phylogenetic trends are observed in the P1 element of *Cornudina*.

(2) *Cornudina* shares only few similarities with Gondolellidae; although likely to represent the P1 element of an apparatus of the Order Ozarkodinida Dzik (1976), questions concerning the apparatus of *Cornudina*, as proposed in Koike (1996) and Orchard (2005), remain.

(3) The variability within the accepted apparatus symbols P1, P2, M, S0, S1, S2, S3, S4, not only represents the key to supra-generic classification, but may also result from some evolution within the elements of the apparatus in the course of the Triassic, for which the introduction of new genera such as *Ketinella* and additional form-species signal the morphological differences.

(4) The alternative ramiform elements may correspond to skeletal elements of Orchard's (2005) *Cornudina* multi-element.

(5) The form genera *Ketinella* Gedik (1975) and *Kamuellerella* Gedik (1975) are alternative

ramiform skeletal elements of the hypothetical multielement apparatus of *Cornudina*, as proposed by Orchard (2005).

(6) The newly described *Gedikella quadrata* gen. nov., sp. nov., is an S element, *Kamuellerella rectangularis* sp. nov., is either an S3 or an S4 element, and *Ketinella goermueshi* sp. nov., is an M element.

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