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A subcircular insect wing from the Late Carboniferous of Osnabrück, Germany

CARSTEN BRAUCKMANN & KARL JOSEF HERD

Abstract: A peculiar isolated subcircular wing of an evidently giant “palaeopterous” insect from the Late Carboniferous (Pennsylvanian: Westphalian D) of the Piesberg near Osnabrück (Lower Saxony, Germany) is described and discussed. There are two main alternative interpretations: (1) a prothoracic winglet, and (2) a reduced metathoracic (hind) wing as is, for example, common in Recent Ephemeroptera. Bearing in mind the large size, the first interpretation is slightly preferred here, but other possibilities cannot completely be excluded.

Key words: Insecta, “Palaeoptera”, wing, subcircular shape, Late Carboniferous (Pennsylvanian), Osnabrück area, interpretation

Kurzfassung: Ein eigentümlicher isolierter, subzirkulärer Flügel von einem offensichtlich riesigen „palaeopteren“ Insekt aus dem Ober-Karbon (Pennsylvanium: Westfalium D) vom Piesberg bei Osnabrück wird beschrieben und diskutiert. Bei der Interpretation bestehen zwei Haupt-Möglichkeiten: (1) als Prothoracal-Flügel und (2) als verkürzter Metathoracal-Flügel, wie sie unter anderem auch bei rezenten Ephemeroptera verbreitet sind. Wegen der bedeutenden Größe wird die erste Deutungs-Möglichkeit leicht bevorzugt, wenngleich andere Möglichkeiten nicht völlig ausgeschlossen werden können.

Schlüsselwörter: Insecta, „Palaeoptera“, Flügel, subzirkulärer Umriss, Ober-Karbon (Pennsylvanium), Raum Osnabrück, Interpretation

1 Introduction

Several years ago the palaeobotanist Professor Dr. Hans Kerp (Münster) drew our attention to a peculiar, large, subcircular insect wing which he collected from the Late Carboniferous (Pennsylvanian; Westphalian D) sequence in the Piesberg Quarry N Osnabrück (Lower Saxony, Germany). Since he could easily discount the fossil from being a plant by the very different, much more regular venation, he supposed that it could be an insect wing and ceded it to us for study. In spite of the fact that it was already in our care when we prepared parts 1 and 2 of the monograph of the Late Carboniferous insects of the Piesberg locality (BRAUCKMANN & HERD 2003 and 2006), we decided then not to include it because of its doubtful systematic position and the need for detailed discussions.

Although not unique, the shape of this wing is so unusual that we scheduled a separate article for its description and discussion. Due to the different possibilities for interpretation, as well as the uncertain

systematic position, we prefer not to give the fossil a scientific name.

2 Terminology

The terminology of the here supposed wing venation is the same as used in BRAUCKMANN & HERD (2003 and 2006) and follows KUKALOVÁ-PECK (1983) and KUKALOVÁ-PECK & RICHARDSON (1983): RA = Radius anterior, RP = Radius posterior; MA = Media anterior, MP = Media posterior; CuA = Cubitus anterior, CuP = Cubitus posterior; AA = Analis anterior, AP = Analis posterior.

3 Systematics and description

“Palaeoptera MARTYNOV, 1923”

Remarks: If Neoptera have their origins among the “Palaeoptera”, as supposed by many palaeoentomol-

ogists, then “Palaeoptera” are paraphyletic and thus artificial. Here this name is used not in the sense of phylogenetic systematics, but only as group of early insects with “palaeopterous” wing folding. As far as is known, “Palaeoptera” includes Diaphanopteroidea, Palaeodictyoptera, Megasecoptera, Permithermistida, Ephemeroptera and Odonatoptera. The whole complex of “Palaeoptera” requires careful revision using modern phylogenetic approaches.

With certain giant Palaeodictyoptera (in particular Homiopteridae), Ephemeroptera (Bojophlebiidae), and Odonatoptera (like for example the Meganisoptera: Meganeuridae) the “Palaeoptera” include the largest Pterygota of all. Many species have well-developed prothoracic wings with homologous venation to the mesothoracic and metathoracic wings. Additionally, more advanced Ephemeroptera have reduced subcircular metathoracic wings. Therefore selected “palaeopterous” insects have to be included in the discussion.

?Palaeodictyoptera or ?Ephemeroptera

Large subcircular wing of a giant “palaeopterous” insect (Fig. 1A-B)

Material: Specimen IGP In 189, deposited in the collection of the Institut für Geologie und Paläontologie, TU Clausthal (Clausthal University of Technology).

Locality: Piesberg Quarry N Osnabrück, Lower Saxony, northern Germany.

Stratum: Late Carboniferous (Pennsylvanian),

Westphalian D (without exact allocation to one of the seams in this part of the section).

Preservation: Fragment of a large subcircular wing with the anteriormost region (most probably the anteradial area including RA) not visible and the posterior-proximal region (most probably a large part of the anal area) broken off. Venation and branching marked and well preserved. Main veins with trachea-shaped appearance. Corrugation not clearly developed.

Measurements (in mm): Preserved length from base to apex = 56; preserved width = 55. The size of the complete wing is estimated to have shown slightly larger dimensions. In particular, with respect to the distances of the main veins in the proximal part (with the veins running nearly together towards the base) the length and width should be slightly longer.

Description: Shape of wing subcircular, nearly circular, with bluntly rounded apical region (slightly truncated). Five main veins preserved rather regularly and dichotomous; here interpreted as representing most probably RP to AA, but without well-developed corrugation (interpretation therefore equivocal). RP with six terminal branches. MA only shortly branched near margin; MP with five terminal branches, probably orientated along the wing axis. CuA with six, CuP with five terminal branches. AA incompletely preserved, only two terminal branches visible. No cross veins and no archaedicton present.

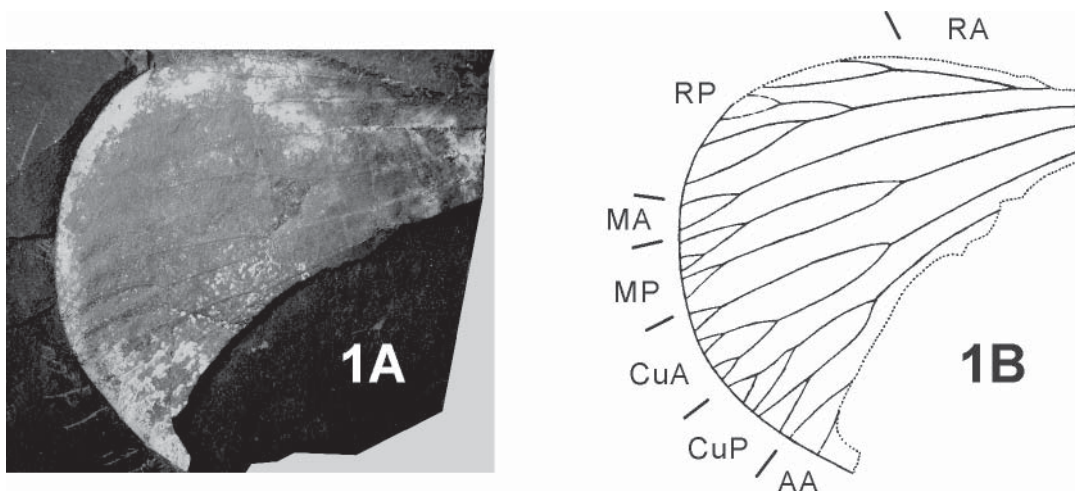


Fig. 1: Large subcircular wing of a giant “palaeopterous” insect, IGP In 189; Late Carboniferous (Pennsylvanian; Westphalian D), Piesberg near Osnabrück (Lower Saxony, Germany). – 1A: Photograph. – 1B: Drawing. – Original size (preserved length of wing = 56 mm).

4 Discussion

The shape and dimensions of the present wing are unusual, but not unique. SCUDDER (1868), GOLDENBERG (1873) and KLIVER (1886) previously described and figured similar large subcircular insect wings from the Late Carboniferous (Pennsylvanian). SCUDDER's material, named *Megathentomum pustulatum* SCUDDER, 1868 (Fig. 6 in the present article), came from the Westphalian D of Mazon Creek in Illinois (USA) and was refigured by HANDLIRSCH (1906) who additionally differentiated a second species among the Mazon Creek fauna: *M. scudderi* HANDLIRSCH, 1906 (Fig. 7 in the present article).

The specimens described by the two other authors [*Acridites formosus* GOLDENBERG, 1873 and *A. goldenbergi* KLIVER, 1886, Figs. 3 and 4 in the present article, respectively] were collected from sediments of Westphalian D age in the Saar and are nearly contemporaneous with both the Mazon Creek specimens and with the new Piesberg wing.

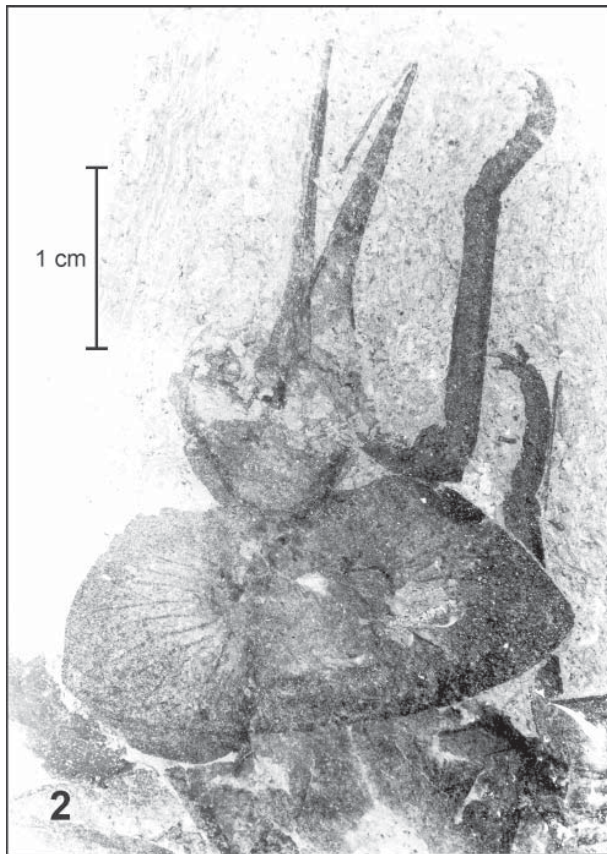


Fig. 2: *Homioptera vorhallensis* BRAUCKMANN & KOCH, 1982 (Palaeodictyoptera: Homiopteridae), Late Carboniferous (Pennsylvanian; Late Namurian B, Marsdenian), Hagen-Vorhalle (North Rhine-Westphalia, Germany). Head and prothoracic region with winglets displaying the venation, for comparison with the Piesberg specimen. From BRAUCKMANN (1991: 199).

The Saar examples were subsequently refigured by HANDLIRSCH (1906), who introduced two new generic names for them [*Paracridites* and *Pseudacridites*, respectively]. GUTHÖRL (1934) contributed further comments on the Saar species.

The following interpretations for the Piesberg specimen have to be discussed:

(1) Prothoracic wing of a giant “palaeopterous” member of the Pterygota, most probably of the Palaeodictyoptera,

(2) shortened subcircular metathoracic wing, again of a giant “palaeopterous” member of the Pterygota, maybe of the Palaeodictyoptera or the Ephemeroptera,

(3) shortened and truncated mesothoracic wing of a still unknown giant member of the Neoptera (perhaps moving towards elytrisation),

(4) pathology or genetic defects.

(1) Already BRONGNIART (1893) interpreted the wing of *Megathentomum pustulatum* as a prothoracic wing of a giant insect. HANDLIRSCH (1906: 322) was undecided on this question, but did not reject it, and GUTHÖRL (1934) came to a similar opinion, but also noted that he preferred to allocate these subcircular wings to a “more advanced group of insects”.

Such giant insects with well-developed prothoracic wings are common in certain “palaeopterous” groups of Pterygota, like for example among Palaeodictyoptera, in particular within the Homiopteridae. In this family the venation is often clearly visible (Figs. 2 and 5) and still resembles the ground-plan of the pro-wing as postulated by KUKALOVÁ-PECK (1983) (Fig. 8 in the present article). The venation pattern of the Piesberg specimen (Fig. 1B) is typical for homiopterid mesothoracic and metathoracic wings which are characterized by a simple MA and a more or less branched CuA. By contrast, the smaller prothoracic winglet of *Homioptera gigantea* AGNUS, 1902 (Fig. 5) has a simple MA and CuA. The analogous winglets of *Homioptera vorhallensis* BRAUCKMANN & KOCH, 1982 (Fig. 2 in the present article) are more similar with regard to wing shape and the branching of the veins. For four specimens of *H. vorhallensis* details and data of the prothoracic venation pattern are listed (see BRAUCKMANN 1991: tab. 2). This venation is homologous to its mesothoracic and metathoracic wings. It appears that the main veins RP, MA, MP, etc. of the new Piesberg winglet are not derived from the common R, M or Cu stems as also figured for the other prothoracic wings in question. The ScP, RA, RP, MA, MP, CuA, CuP, AA and AP veins probably

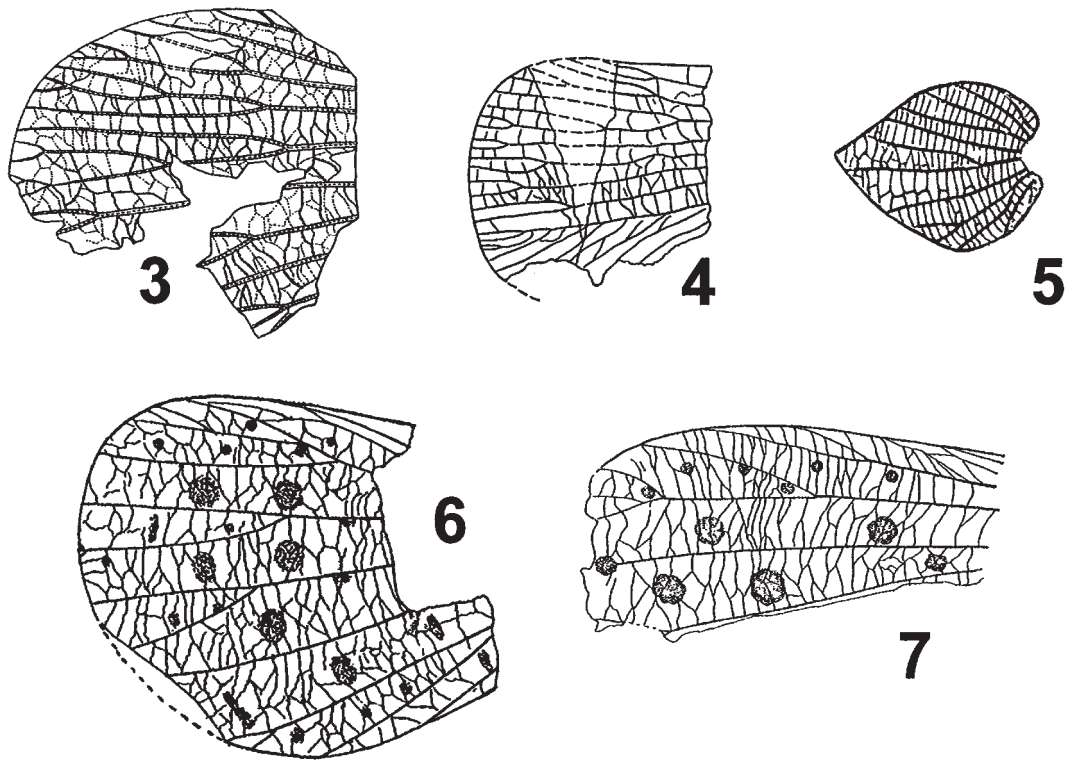


Fig. 3-7: Selected different large subcircular wings (of doubtful systematic position) in original size, for comparison with the Piesberg specimen. – 3: *Paracridites formosus* (GOLDENBERG, 1873), Late Carboniferous (Pennsylvanian; Westfalian D), dump in the Fischbach-Tal, material originating from Jägersfreude Colliery (Saar, Germany). From GUTHÖRL (1934: 167). – 4: *Pseudacridites goldenbergi* (KLIVER, 1886), Late Carboniferous (Pennsylvanian; Westfalian D), dump in the Steinbach-Tal, material originating from von der Heydt Colliery (Saar, Germany). From GUTHÖRL (1934: 169). – 5: *Homoioptera gigantea* AGNUS, 1902, Late Carboniferous (Pennsylvanian; Stephanian B, Commeny (Central France), prothoracic winglet. From KUKALOVÁ-PECK & RICHARDSON (1983: 1685). – 6: *Megathentomum pustulatum* SCUDDER, 1868, Late Carboniferous (Pennsylvanium; Westphalian D), Mazon Creek (Illinois, USA). From HANDLIRSCH (1906: pl. 33 fig. 15). – 7: *Megathentomum scudderi* HANDLIRSCH, 1906, Late Carboniferous (Pennsylvanium; Westphalian D), Mazon Creek (Illinois, USA). From HANDLIRSCH (1906: pl. 33 fig. 16).

originated at the wing base from the basal plates. In some cases the base shows the maximum width of the winglet [e.g. Lycocercidae, see KUKALOVÁ (1969), and the hypothetical pro-wing (Fig.8)].

A giant specimen of Homiopteridae with strong affinities to *Mazonopterus wolfforum* KUKALOVÁ-PECK & RICHARDSON, 1983 has also recently been collected in the Piesberg Quarry and will be described in future. But in contrast to the subcircular wings discussed here, most of the prothoracic wings of the Palaeodictyoptera are more heart-shaped, with a pointed apex, and show a large number of cross veins. One example of an approximately semi-circular prothoracic wing is *Lithomantis carbonaria* WOODWARD, 1876 (Palaeodictyoptera) from the Coal Measures (Westphalian) near Ayr, Strathclyde (Scotland).

Truly semicircular, but small, prothoracic wing pads (maximum width at the base) are known from the Permian *Lemmatophora typa* SELLARDS, 1909 (Lemmatophoridae) and other related “grylloblatoid” families and are perfectly figured and described as reticulate pronotal lobes by CARPENTER (1992: 98). These much smaller animals are examples of typical prothoracic winglets in Neoptera which differ clearly by the reticulate venation.

That the new Piesberg specimen most probably belongs to a giant “palaeopterous” insect is indicated by the size ratio between prothoracic and meso/metathoracic wings for a number of more completely preserved Palaeodictyoptera. The length ratio of these wings of *H. vorhallensis* (prothoracic wing: 1 ~ 16 mm; w ~ 16 mm) is roughly 1 : 5, the width ratio roughly 1 : 2. As figured for *H. gigantea* or *L.*

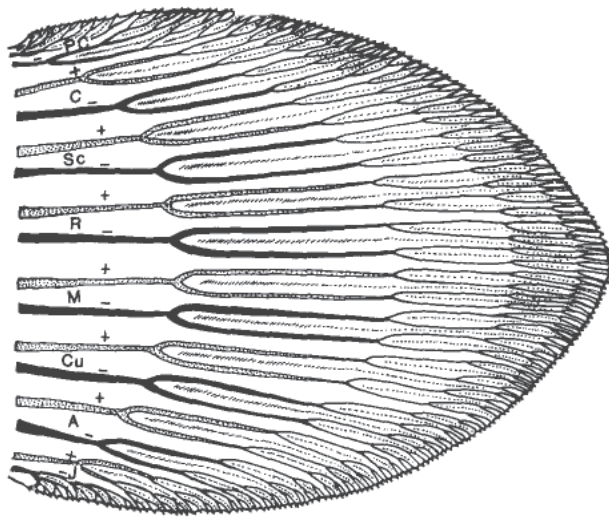


Fig. 8: Model of a hypothetical, more or less symmetrical pro-wing, for comparison with the Piesberg specimen. From KUKALOVÁ-PECK (1983: 1637). Without scale.

carbonaria length ratios of 1 : 8 are possible.

Thus a length of at least 300 mm can be estimated for the corresponding mesothoracic and metathoracic wings of the Piesberg specimen. Nevertheless, it has to be considered that at an early stage of evolution a relatively large “palaeopterous” prothoracic wing was developed in a length ratio of one to three or two and hence the estimated size of the Piesberg insect (span width) would have to be reduced.

(2) Shortened or even largely reduced metathoracic wings seem to be even present in Carboniferous Pterygota, at least for example in *Valdeania medeirosi* TEIXEIRA, 1941 (Fig. 9) [Palaeodictyoptera: Eugereonidae] from the Stephanian of northern Portugal. But judging from the strong tectonic distortion of other insect wings from this locality, we cannot exclude the possibility that the obvious disproportions between the mesothoracic and metathoracic wings in this species are caused largely by tectonic processes. A similar degree of disproportion is documented in *Zessinella siope* BRAUCKMANN, 1988 [Odonatoptera] from the Namurian B (Marsdenian) of Hagen-Vorhalle (Germany).

In the hitherto known Palaeozoic species of the Ephemeroptera the mesothoracic and metathoracic wings are rather similar in shape and venation. However, drastic reduction or a subcircular shape of the metathoracic wings is common in more advanced Ephemeroptera from younger stratigraphical ages (see for comparison the Recent North American *Baetisca* sp., Fig. 10).

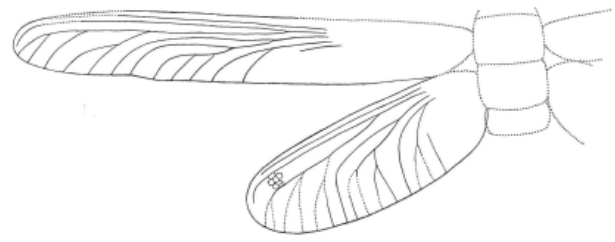


Fig. 9: *Valdeania medeirosi* TEIXEIRA, 1941 (Palaeodictyoptera: Eugereonidae), Late Carboniferous (Pennsylvanian; Stephanian), Pôrto, northern Portugal; species with presumably shortened metathoracic wing (maybe caused by tectonic distortion?). From TEIXEIRA, (1941: 15; modified by E. GRÖNING). Length of mesothoracic wing (estimated) = 64 mm.

(3) Shortened and subtruncate mesothoracic wings also occur in several groups of Neoptera, in particular in cases of increasing elytrisation (like for example *Protoprosbole straeleni* LAURENTIAUX, 1952). But as far as we know, all these species are not as large as the Piesberg specimen and the other species here under discussion. Then there should also be expected occasional (but of course not guaranteed) records of extremely large metathoracic wings which could have been densely folded to get protected under such “elytrae” or pre-elytran conditions. This is not yet the case.

(4) Shortening of the wing by occasional genetic modification, mutation or pathological reasons maybe possible, but cannot be proved by the present palaeontological methods. Furthermore, this situa-

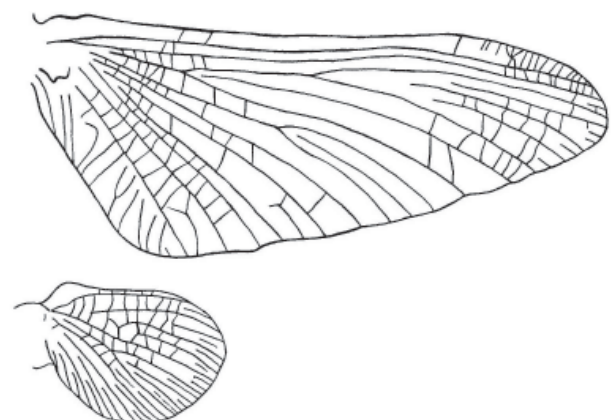


Fig. 10: *Baetisca* sp., Recent, North America (Ephemeroptera: Baetiscidae), mesothoracic wing and remarkably reduced subcircular metathoracic wing, for comparison with the Piesberg specimen. From ILLIES (1968: 15; modified by E. GRÖNING). Scale not indicated in the original publication.

tion should be extremely unlikely, due to the generally poor conditions of fossilisation in Pterygota. Even if there is only one single specimen known in the fossil record, the species is to be expected as quite common during its time of life. How much less probable must it be to collect a specimen with such rare peculiarities.

5 Conclusions

After careful considerations of all the arguments mentioned above, we tend towards interpreting the large subcircular wings as prothoracic wings of giant “palaeopterous” Pterygota (as for example giant Homiopteridae) rather than as a shortened metathoracic wing of a likewise giant species of “palaeopterous” insects (as is common in advanced Ephemeroptera and also probably known from certain Palaeodictyoptera).

Less likely – but impossible to exclude – is its interpretation as a shortened subtruncate mesothoracic wing. Even in this case the animal must have been of giant dimensions.

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Authors' adresses:

Prof. Dr. Carsten Brauckmann,
 Institut für Paläontologie,
 TU Clausthal (Clausthal University of Technology),
 Leibnizstraße 10,
 D-38678 Clausthal-Zellerfeld,
 e-mail: Carsten.Brauckmann@tu-clausthal.de

Dr. Karl Josef Herd,
 Am Gartenfeld 66,
 D-51519 Odenthal-Holz,
 E-mail: Herd.Carlo@t-online.de