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THE STRATIGRAPHICAL POSITION OF THE OLDEST KNOWN PTERYGOTA (INSECTA. CARBONIFEROUS, NAMURIAN)

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(4 figures)

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ABSTRACT. The stratigraphical position of some Namurian pterygote insects is reviewed. The oldest hitherto known species is *Delitzschala bitterfeldensis* C. Brauckmann & Schneider, 1995 (in press) from Lower Namurian A (Arnsbergian, E2) strata of the Bitterfeld/Delitzsch area, Germany. Due to the new definition of the Mid-Carboniferous boundary, this sequence now belongs to the Lower Carboniferous part of the Namurian. The other Namurian pterygotes come from the Upper Carboniferous part. *Ampeliptera limburgica* Pruvost, 1927 from the South Limburg coal-field (the Netherlands) is most probably of Upper Namurian A (Alportian) age. Two species, *Stygne roemeri* Handlirsch, 1906 from Upper Silesia (Poland) and *Brodioptera stricklani* Nelson & Tidwell, 1988 from Utah (USA), can tentatively be allocated to Lower Namurian B (Kinderscoutian) strata. All further certain Namurian species are younger (Marsdenian to Yeadonian). The previously supposed Lower Namurian age of *Eugeropteron lunatum* Riek, 1984 and *Geropteron arcuatum* Riek, 1984 from Malanzán, Argentina, as well as of *Xenoptera riojaensis* Pinto, 1986 from the same locality is not certain; an early Westphalian age for these species appears more likely.

KEYWORDS: Pterygote insects, Carboniferous, Namurian.

RESUME. La position stratigraphique des plus ancien Ptérygotes connus (insectes; Carbonifère, Namurien). La position stratigraphique de quelques insectes ptérygotes du Namurien est revue. La plus ancienne espèce connue est *Delitzschala bitterfeldensis* C. Brauckmann & Schneider (1995); elle provient du Namurien A inférieur (Arnsbergien, E2) de la région de Bitterfeld/Delitzsch (Allemagne). En raison de la nouvelle définition adoptée pour la limite Mi-Carbonifère, cette séquence appartient maintenant à la partie d'âge carbonifère inférieur du Namurien. Pour autant que l'on puisse le déduire des travaux antérieurs, les autres ptérygotes namuriens proviennent de la partie d'âge carbonifère supérieur. *Ampeliptera limburgica* Pruvost, 1927 du bassin houiller du sud du Limbourg (Pays-Bas) est très probablement d'âge Namurien A supérieur (Alportien). Deux espèces pourraient être attribuées aux strates du Namurien B inférieur (Kinderscoutien): *Stygne roemeri* Handlirsch, 1906 (Pologne) et *Brodioptera stricklani* Nelson & Tidwell, 1988 (Utah, USA). Toutes les autres espèces du Namurien sont plus récentes (Marsdenien à Yeadonien). L'âge namurien inférieur attribué antérieurement à *Eugeropteron lunatum* Riek, 1984 et *Geropteron arcuatum* Riek, 1984 (Malanzán, Argentine), ainsi qu'à *Xenoptera riojaensis* Pinto, 1986 de la même localité n'est pas certain; un âge westphalien ancien semble plus probable pour ces trois espèces.

MOTS-CLES: Carbonifère, Namurien, insectes, ptérygotes.

1. INTRODUCTION

The geological record of hexapods begins about 400 million years ago in the Lower Devonian. All specimens of doubtless Devonian age belong to apterygote hexapods (Collembola and Archaeognatha) since some fossils from the Upper Devonian of Russia previously interpreted as pterygote insects have now been identified as uropods of eumalacostrcan crustaceans (Hennig, 1981: 50). The oldest known pterygotes are of Namurian age and thus distinctly younger. But the presence of several different orders already in the Namurian clearly suggests that the evolution of pterygotes started much earlier, at least in the early Devonian.

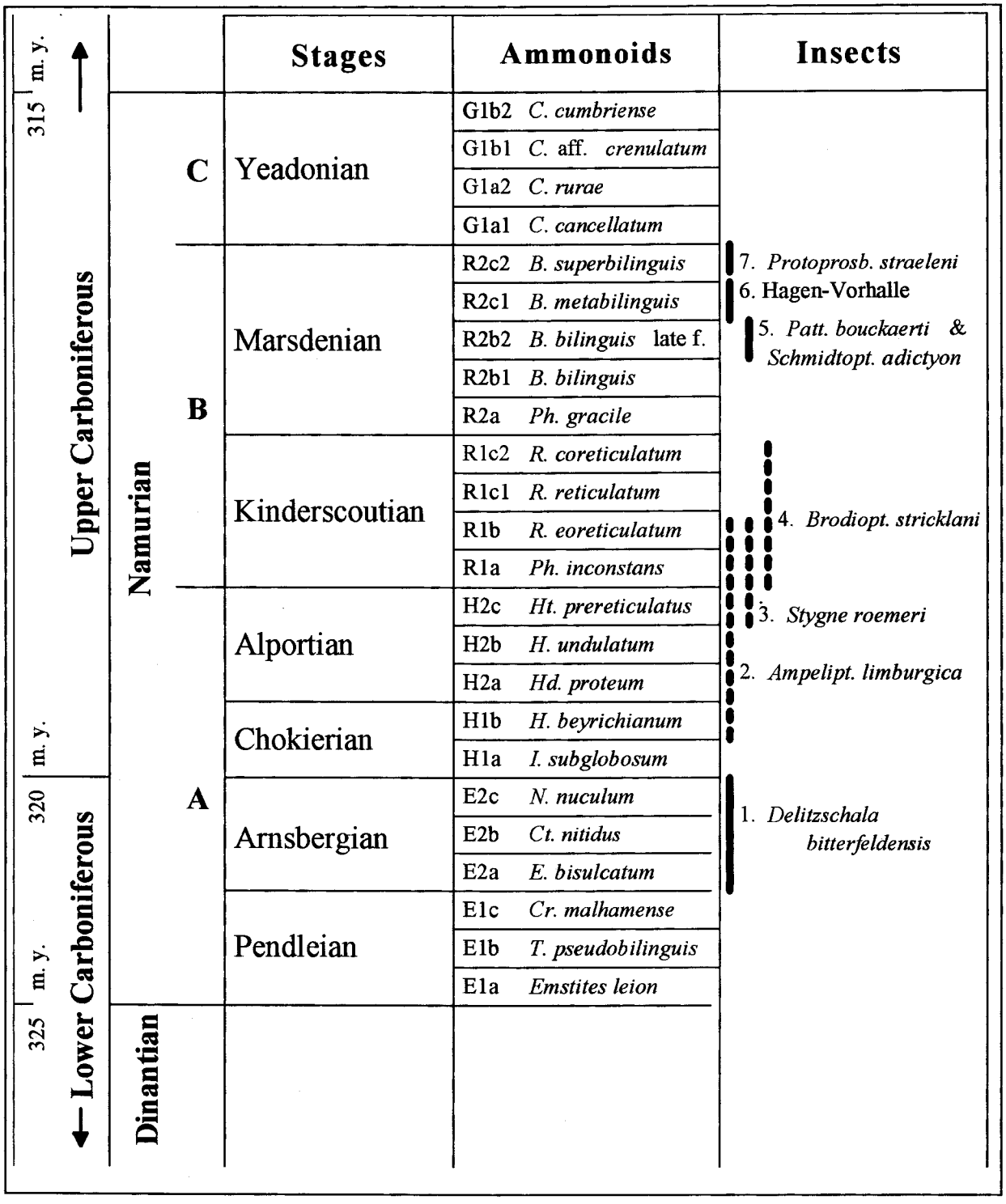

Figure 1. Stages and ammonoid stratigraphy of the Namurian (according to Riley, 1987, partially modified by D. Korn, written communication), and the stratigraphical distribution of the oldest known pterygote insects. - *B.* = *Bilinguites*; *C.* = *Cancelloceras*; *Cr.* = *Cravenoceras*; *Ct.* = *Cravenoceratoides*; *E.* = *Eumorphoceras*; *H.* = *Homoceras*; *Hd.* = *Hudsonoceras*; *Ht.* = *Homoceratoides*; *I.* = *Isohomoceras*; *N.* = *Nuculoceras*; *Ph.* = *Phillipsoceras*; *R.* = *Reticuloceras*; *T.* = *Tumulites*.

In comparison with other groups, fossil insects are very rare. A greater frequency is restricted to very few outstanding localities. For the Carboniferous these are in particular: Commentry and Montceaules-Mines, both in Central France and of Stephanian age, and Mazon Creek in Illinois (USA; Upper Westphalian). Until the discovery of the rich insect fauna of Hagen-Vorhalle in the Rhenish Massif (with more than 150 specimens) only very few remains from Namurian strata have been described. The greatest number (about 20 specimens, mainly isolated wings) had previously been collected from uppermost Namurian (Yeadonian) sediments in the Moravian part of the Upper Silesian coal district. The age of this occurrence has not been seriously doubted and therefore it is not considered herein. The few other localities have yielded only a single or, at best, very few isolated wings.

The problems of the stratigraphical dating of the oldest known (Namurian) pterygote insects are now again of interest since the Mid-Carboniferous boundary has recently been redefined. Previously, in Europe it was connected with the base of the Namurian A and thus with the base of the Pendleian. According to Wagner & Winkler Prins (1994) however, the base of the Upper Carboniferous is now defined by the first appearance of the conodont species *Declinognathodus noduliferus* (Ellison & Graves, 1941). This corresponds approximately with the first occurrence of the ammonoid species *Isohomoceras subglobosum* (Bisat, 1924) at the base of the Chokierian. Thus the early part of the Namurian A (= Pendleian and Arnsbergian) now belongs to the Lower Carboniferous whereas the younger part (= Chokierian) still remains within the Upper Carboniferous (see Fig. 1). This could imply that there are Lower Carboniferous components within the Namurian insect record.

Previously the stratigraphical position of the hitherto known earliest pterygote insects was interpreted rather differently. This applies especially to *Stygne roemeri* Handlirsch, 1906, and *Ampeliptera limburgica* Pruvost, 1927 which were alternately thought to be the oldest insect (see Pruvost, 1927; Rüschkamp, 1928; Schwarzbach, 1939; Haupt, 1940; Kukalová, 1958; Brauckmann, 1988 and 1991). These differences mainly result from the fact that the original datings have been carried out at earlier times ofCarboniferous stratigraphical research when the subdivisions were not very precise. The datings have been based upon the index ammonoids occurring within, above or below the section where the insects have been found. With respect to the enormous splitting within the systematics of ammonoids, the older determinations are in need of a major revision; today they are only of approximate value. As far as can be evaluated from older data, none of the insect specimens mentioned above is of Lower Carboniferous age.

For three recently discovered species, *Eugeropteron lunatum* Riek, 1984, *Geropteron arcuatum* Riek, 1984, and *Xenoptera riojaensis* Pinto, 1986, the difficulties are caused by the regional position of their common collection site in Argentina and thus within Gondwanaland. The stratigraphical position of this part of the section cannot be exactly correlated with the international standard sequence (Wagner & Winkler Prins, 1994). Previous datings vary from Lower Carboniferous or even Devonian to Uppermost Carboniferous, gravitating to possibly ?Lower Namurian. According to quite recent attempts of correlation, such an early dating is not very likely, however.

Insects of probably Late Namurian age are also known from North America (Durden, 1984). Schneider & Werneburg (1993), however, interpreted the data given by Durden (1984) even generally as "drastic miscorrelations". The Namurian species referred to are not considered in the present paper because they seem to be at least slightly younger than the oldest European ones.

A detailed review of the stratigraphical positions of Namurian insects has been presented by Brauckmann & Brauckmann (1992). Since then we have received the first pterygote insect of unequivocally Lower Carboniferous age for study, *Delitzschala bitterfeldensis* C. Brauckmann & Schneider, 1995, from an Arnsbergian sequence of a borehole in the Bitterfeld/Delitzsch area of East Germany (s. Steinbach, 1990; C. Brauckmann & Schneider, 1995). For this reason a modified review is provided here.

2. DATINGS

2.1. *Delitzschala bitterfeldensis* C. Brauckmann & Schneider, 1995 (Fig. 2A) [*Palaeoptera:* Palaeodictyoptera: Spilapteridae Handlirsch, 1906].

Locality. Boring in the northern part of the deposits of the "Sandersdorf-Folge" ("Profil-Typ 2" in Steinbach, 1990: fig. 12) in the Bitterfeld/Delitzsch area (close to Bitterfeld), Germany.

Age. *Delitzschala bitterfeldensis* has been collected from the lower part of the "Sandersdorf-Folge". After the occurrence of certain associated fossil plants - for example, *Lyginopteris bartonicii* (Stur) Patteisky and *L. porubensis* (Trapl) Gothan - Steinbach (1990: 78) placed this part in the E2 zone of the ammonoid sequence and thus in the Arnsbergian which now represents the uppermost part of the Lower Carboniferous. According to Steinbach (1990: 78-79), this

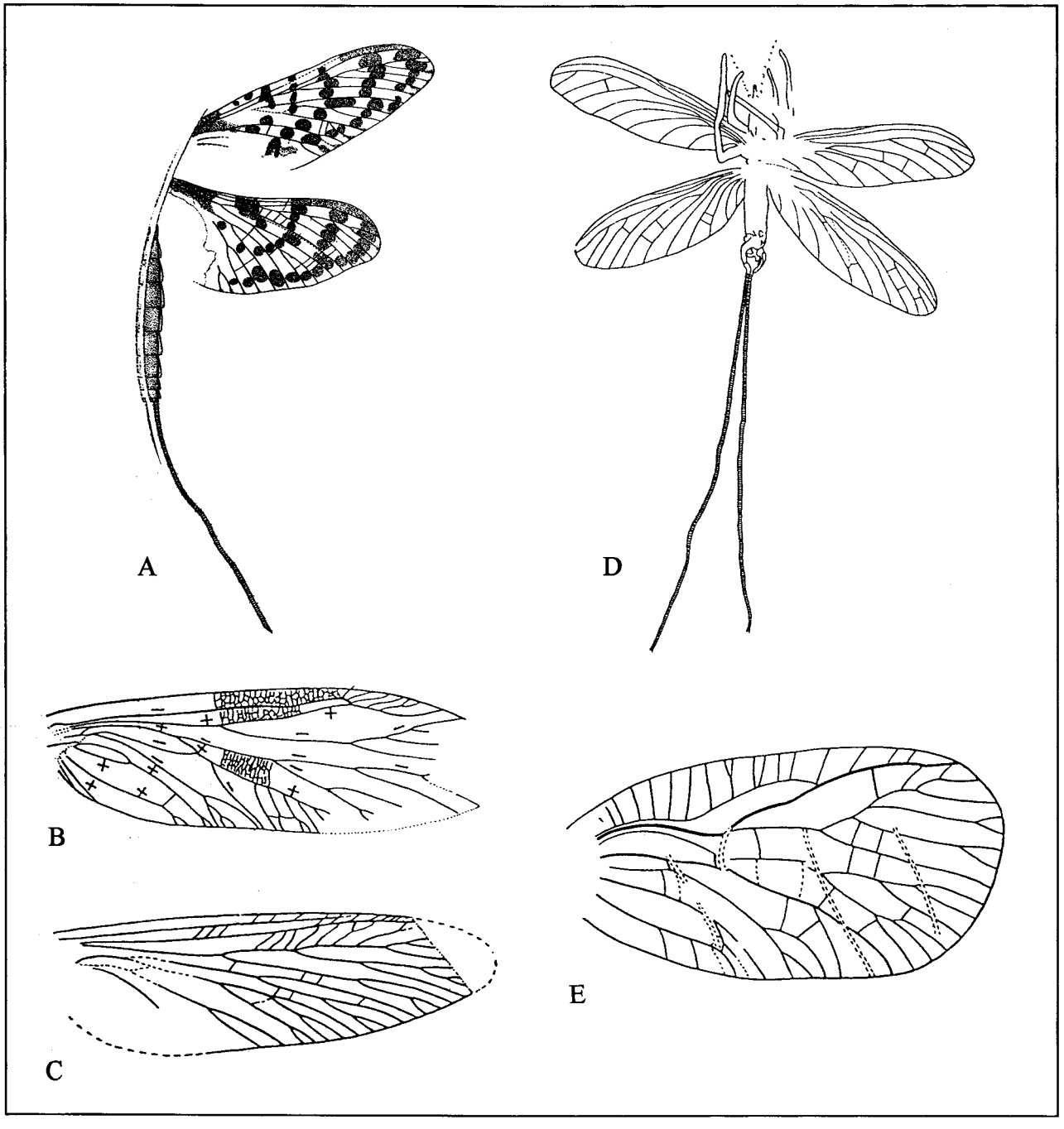

Figure 2. Namurian pterygote insects. A. *Delitzschala bitterfeldensis* C. Brauckmann & Schneider, 1995, right wings (length of mesothoracic wing 11 mm), posterior part of the abdomen with right cercus, Arnsbergian (early Namurian A), Bitterfeld/Delitzsch area, Germany (from C. Brauckmann & Schneider, 1995). B. *Ampeliptera limburgica* Pruvost, 1927, mesothoracic wing (length 10 mm), probably Alportian (latest Namurian A), South Limburg, The Netherlands (from Kukalová-Peck & C. Brauckmann, 1992). C. *Stygne roemeri* Handlirsch, 1906, mesothoracic wing (length approximately 28 mm), probably early Kinderscoutian (earliest Namurian B), Upper Silesian Coal Basin, Poland (modified from Haupt, 1940). D. *Brodioptera stricklani* Nelson & Tidwell, 1988, nearly completely preserved specimen (length of mesothoracic wings 28 mm), probably Kinderscoutian (early Namurian B), Utah, USA (from Nelson & Tidwell, 1988). E. *Protoprosbole straeleni* Laurentiaux, 1952, mesothoracic wing (length 14 mm), early Marsdenian (higher Namurian B), Charleroi area, Belgium (from Laurentiaux, 1952).

dating is confirmed by the recently discovered brachiopods and conchostracs *Orbiculoidea* cf. *marianka* Rehor & Rehorová, 1972 and *Dolicholeaia namuriana* Pribyl, 1960, respectively.
Remarks. *Delitzschala bitterfeldensis* is the hitherto first exactly datable Lower Carboniferous pterygote insect.

2.2. *Ampeliptera limburgica* Pruvost, 1927 (Fig. 2B) [Neoptera: ancestral Hemipteroidea: Ampelipteridae Haupt, 1940].

Locality. Boring at Gulpen (= boring no. 106), South Limburg, The Netherlands (depth: -245 m).

Age. According to Pruvost (1927: 76), the isolated mesothoracic wing comes from a marine horizon in the transition beds between the zone of *Reticuloceras reticulatum* (Phillips, 1836) and the so-called "Ampélites de Chokier (H1a)" and is associated with ammonoids. Today the H1a subzone - characterized by *Isohomoceras subglobosum* - is allocated to the Lower Chokierian and thus to the earliest Upper Carboniferous; *R. reticulatum* is the index ammonoid of the higher Kinderscoutian (R1c1). Therefore the data limit the maximal time interval in which the stratum typicum has to be searched. After Dorsman (1945: 67 and 68), in the Gulpen boring no. 106 *I. subglobosum* occurs at the depth of -310 m and thus at least 65 m below the stratum typicum of *Ampeliptera limburgica*, whereas the first occurrence of *R. reticulatum* at -200 m is distinctly (at least 45 m) above it. In consideration of the fact that generally the sediment thickness is greately increasing since the Kinderscoutian, the age of *Ampeliptera limburgica* can be approximately restricted to the Alportian (Late Namurian A) or Early Kinderscoutian (Early Namurian B).

Remarks. *Ampeliptera limburgica* was regarded as the oldest known pterygote insect by Pruvost (1927), Rüschkamp (1928), and Keller (1938) whereas Schwarzbach (1939) doubted this opinion and favoured *Stygne roemeri* instead. Haupt (1940) and Kukalová (1958) followed Schwarzbach. While considering new stratigraphical charts, Brauckmann (1988 and 1991) was inclined to agree with Pruvost in regarding the South Limburg species as the older one, which was confirmed in detail at first by Brauckmann & Brauckmann (1992). After the discovery of *Delitzschala bitterfeldensis* however, *Ampeliptera limburgica* has lost its rank as oldest pterygote.

The systematic position of *Ampeliptera limburgica* was discussed controversially for a long time, too; the varied history has been reported by Kukalová-Peck & C. Brauckmann (1992). A re-examination of the venation in the article mentioned has shown that the species represents a separate family, Ampelipteridae Haupt, 1940 *sensu* Kukalová-Peck & C. Brauckmann, 1992, within the Neoptera and belongs to the gerarid line of the hemipteroid assemblage.

2.3. *Stygne roemeri* Handlirsch, 1906 (Fig. 2C) [Neoptera: ancestral Hemipteroidea].

Locality. Alfred Mine between Königshütte and Laurahütte, Upper Silesian Coal Basin, Poland.

Age. Römer (1884) remarks that this isolated mesothoracic wing has been collected about 10 m below the Caroline Seam. According to Schwarzbach (1939), this part of the sequence is contemporary with the Pochhammer (=Prokop) Seam which lies at the base of the "Sattelflöz Group" and is approximately parallelized by Hartung & Patteisky (1960) with the Kaisberg Beds in the Ruhr area. In this case it would belong within the uppermost Marsdenian (R2c) and would be even a little bit younger than the insect-bearing beds of Hagen-Vorhalle. But more recently, Rehor & Rehorová (1972) allocated the beds of the Prokop Seam to the uppermost part of the Ostrava Beds and thus approximately to the lowermost Kinderscoutian (= lowermost Namurian B).

Remarks. The extremely low stratigraphical age of *Stygne roemeri* has been emphasized at first by Schwarzbach (1939) who moreover was of the opinion that it would be at least contemporary with *Ampeliptera limburgica* or even a little bit older. But due to the studies by Rehor & Rehorová (1972) as well as to the data concerning *Ampeliptera limburgica* as given above, both species seem to be approximately contemporary.

2.4. *Brodioptera stricklani* Nelson & Tidwell, 1988 (Fig. 2D) [Palaeoptera: Megasecoptera: Brodiopteridae Carpenter, 1963].

Locality. Near Lehi, Utah Co., Utah, USA.

Age. The exact stratigraphical position of this well preserved specimen from the Manning Canyon Shale Formation is also not clear. Based on the great number of associated Pennsylvanian plants and the few Mississippian floral components, Nelson & Tidwell (1988) concluded an age which approximately correponds with the Kinderscoutian (= Lower Namurian B) in Europe.

Remarks. If the dating is correct, *Brodioptera stricklani* is the oldest known pterygote insect of North America and represents the most ancient megasecopteran species of all, which seems to be nearly contemporary with *Stygne roemeri*.

There is some confusion about the date of publication of *Brodioptera stricklani*. The serial number gives

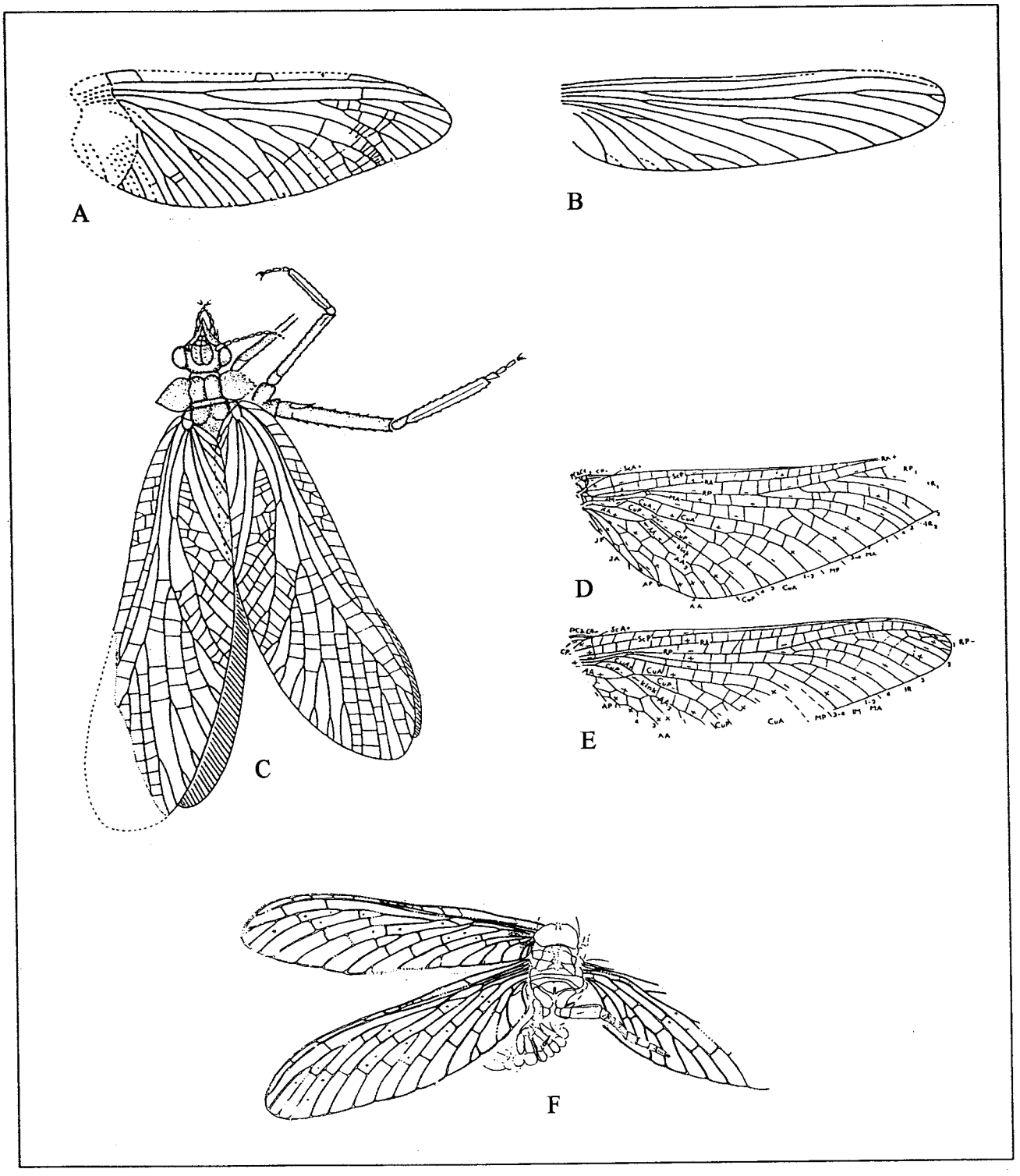

Figure 3. Namurian and probably Westphalian pterygote insects. A. *Patteiskya bouckaerti* Demoulin, 1958, mesothoracic wing (length 55 mm), middle Marsdenian (higher Namurian B), Wuppertal area, Germany (from C. Brauckmann, 1991). B. *Schmidtopteron adictyon* C. Brauckmann & Hahn, 1978, wing (length 29 mm), middle Marsdenian (higher Namurian B), Wuppertal area, Germany (modified from C. Brauckmann & Hahn, 1978). C. *Heterologopsis ruhrensis* C. Brauckmann & Koch, 1982, nearly completely preserved specimen (length of mesothoracic wing 25 mm), late Marsdenian (latest Namurian B), Hagen-Vorhalle, Germany (from C. Brauckmann, 1991). D. *Eugeropteron lunatum* Riek, 1984, metathoracic wing (preserved length 35 mm), probably early Westphalian, Malanzán, La Rioja Province, Paganzo Basin, Argentina (from Riek & Kukalová-Peck, 1984). E. *Geropteron arcuatum* Riek, 1984, metathoracic wing (length 45 mm), probably early Westphalian, Malanzán, La Rioja Province, Paganzo Basin, Argentina (from Riek & Kukalová-Peck, 1984). F. *Xenoptera riojaensis* Pinto, 1986, rather completely preserved specimen (length of mesothoracic wing 27 mm), probably early Westphalian, Malanzán, La Rioja Province, Paganzo Basin, Argentina (from Pinto, 1986).

1987 wheras the date of publication of volume 94 of Psyche is 1988. The latter date is also cited by Ross & Jarzembowski (1993) and is accepted by the present authors, too.

2.5. *Patteiskya bouckaerti* Demoulin, 1958 (Fig. 3A) and ***Schmidtopteron adictyon* C. Brauckmann & Hahn, 1978** (Fig. 3B) [Palaeoptera: Palaeodictyoptera: Graphiptilidae Handlirsch, 1906 and Dictyoneuridae Handlirsch, 1906, respectively].

Locality. Former brickyard quarry at Schmiedestraße N Wuppertal, Germany.

Age. Both isolated wings have been found within the same limited section of the Upper Hagen Beds. According to Patteisky (1959: 48, fig. 12), they can be dated by the associated ammonoids in the R2b2 zone (middle part of the Marsdenian).

Remarks. Until recently, both species represented the most ancient Palaeodictyoptera. In the meantime they have been surpassed by *Delitzschala bitterfeldensis*.

2.6. The pterygote insects from Hagen-Vorhalle (compare Fig. 3C).

Locality. (New) brickyard quarry in Hagen-Vorhalle, Germany.

Age. The insects are associated with the ammonoid species *Bilinguites metabilinguis* (Wright, 1927) and *Anthracoceratites arcuatilobus* (Ludwig, 1863) which indicate a R2c1 zone (higher Marsdenian) age of the Vorhalle Beds.

Remarks. The fossil insect fauna of Hagen-Vorhalle is by far the richest one of Namurian age. Including the recent findings of the exploration by the Münster Natural History Museum, the number of specimens increased to more than 150. A lot of them are nearly completely preserved. Up to now 15 species of 5 orders are described (Brauckmann, 1991): Palaeodictyoptera (6 species), Megasecoptera (1 species), Diaphanopterodea (1 species), Odonata (3 species), and ancestral Hemipteroidea (4 species). For the Diaphanopterodea and the Odonata the Vorhalle specimens are the most ancient ones within the fossil record which can be exactly dated.

2.7. *Protoprosbole straeleni* Laurentiaux, 1952 (Fig. 2E) [Neoptera inc. sed.: Protoprosbolidae Laurentiaux, 1952].

Locality. Charbonnages de Monceau-Fontaine, Charleroi Coal Basin, Belgium.

Age. *Protoprosbole straeleni* is again represented by a single isolated mesothoracic wing. In previous publications, e. g. Laurentiaux (1952), it has been allocated to the Namurian C (= Yeadonian), but Laurentiaux-Vieira & Laurentiaux (1985) - without detailed explanations - corrected it to Lower Marsdenian (higher Namurian B). According to Dusar (written communication), the specimen however has been probably found in uppermost Marsdenian strata just below the base of the Yeadonian (about 3 m below the marine band which could be correlated to "Hauptflöz").

Remarks. The systematic position of *Protoprosbole straeleni* is still completely uncertain. Laurentiaux (1952) placed it as member of the monotypic superfamily Protoprosboloidea into the Homoptera: Auchenorrhyncha: Cicadinea (and therewith directly to the cicads). Other authors - as for example Hennig (1981) - doubted any connection with the Homoptera.

2.8. *Eugeropteron lunatum* Riek in Riek & Kukalová-Peck, 1984 (Fig. 3D), ***Geropteron arcuatum* Riek in Riek & Kukalová-Peck, 1984** (Fig. 3E) [both: Palaeoptera: Odonata: Meganisoptera: Eugeropteridae Riek in Riek & Kukalová-Peck, 1984], and ***Xenoptera riojaensis* Pinto, 1986** (Fig. 3F) [Palaeoptera: Megasecoptera: Xenopteridae Pinto, 1986]

Locality. Cuestita de la Herradura near Malanzán, La Rioja Province, Paganzo Basin, Argentina.

Age. These 3 species are each represented by a single specimen and have been collected from the same beds. According to Azcuy *et al.* (1991) the section belongs to the member 3 of the Malanzán Formation which is subdivided into 4 members. The stratigraphical age of this lacustrine turbidite sequence is not clear. According to Riek & Kukalová-Peck (1984), it at first has been allocated to the Lower Carboniferous or even to the Devonian by lithologic reasons, later - based upon detailed studies of the plant remains - to the late Upper Carboniferous, and at last - after a palynological analysis - it is referred tentatively to the ?Lower Namurian. Thus, after the new definition of the Mid-Carboniferous boundary, these specimens could have been the first Lower Carboniferous records of pterygote insects. But also this opinion has recently been doubted from a paleobotanical point of view (oral communication by Archangelsky, 1991) which more likely suggests a Westphalian age.

Archangelsky *et al.* (1987: 285, chart 14) showed that the Malanzán Formation belongs to a floral unit which is characterized by *Nothorhachis argentinica* (Geinitz) Archangelsky, *Botrychiopsis weissiana*

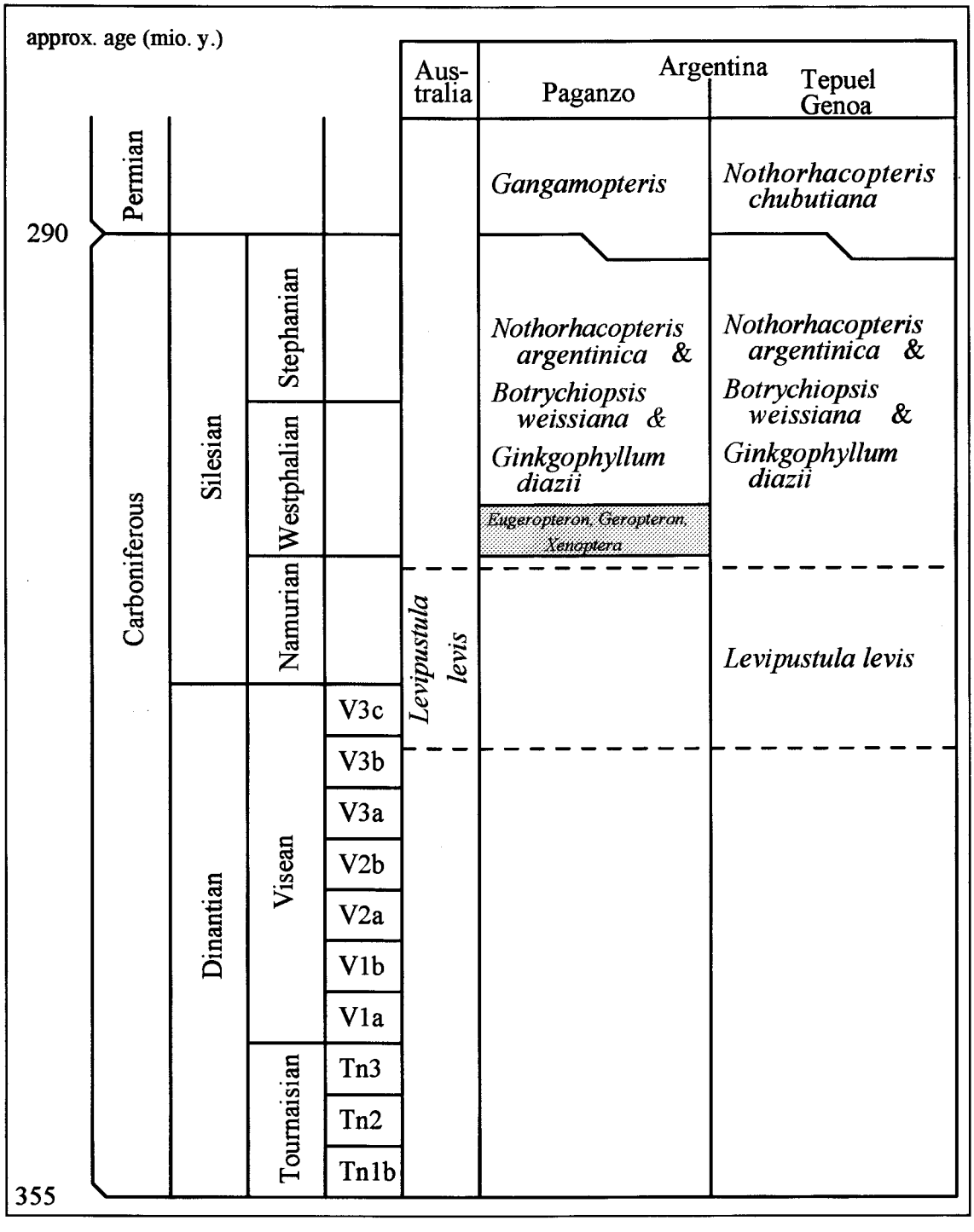

Figure 4. The presumable stratigraphical position of the Malanzán insects, *Eugeropteron lunatum* Riek, 1984, *Geropteron arcuatum* Riek, 1984, and *Xenoptera riojaensis* Pinto, 1986 (La Rioja Province, Paganzo Basin, Argentina). Data combined from Archangelsky *et al.* (1987: 285, chart 14) and from Roberts *et al.* (1993: fig 5).

Kurtz and *Ginkgophyllum diazii* Archangelsky & Arrondo (= NBG). In the Tepuel/Genoa Basin this unit can be approximately parallelized with a sequence which overlies the zone of the brachiopod *Levipustula levis* Maxwell, 1951. According to Roberts *et al.* (1993: Fig. 5), this zone can be restricted in Australia to an interval from the late Visean to the latest Namurian. This suggests that at least the insect-bearing member 3 of the Malanzán Formation seems to be of latest Namurian or - more probably - early Westphalian age (s. Fig. 4).

Remarks. Due to certain characters of the venation of *Eugeropteron lunatum* and *Geropteron arcuatum*, both species seem to be phylogenetically very primitive. There are still close similarities with the Ephemeroptera, the supposed adelphotaxon of the Odonata. From this point of view, an older age would be not surprising.

Though already published in 1986, the almost completely preserved *Xenoptera riojaensis* has been overlooked in several subsequent articles; it even has not been mentioned in the chapter on the Malanzán area in Azcuy *et al.* (1993: 22) who obviously only refer to the odonate insects ["... the type locality for new genera and species, as well as a new insect family"]. If compared with the other two Namurian Megasecoptera - *Brodioptera stricklani* Nelson & Tidwell, 1988 (s. a.; Fig. 2D) and *Sylvohymen peckae* C. Brauckmann, 1988 (from Hagen-Vorhalle; see Brauckmann, 1991: Fig. 48) - *Xenoptera riojaensis* has a distinctly richer venation.

3. CONCLUSIONS

The exact stratigraphical position of the pre-Yeadonian Namurian pterygote insects remain still uncertain and can only approximately allocated to the recently defined stages or to the biozonal units of the ammonoid stratigraphy, i. e. of *Ampeliptera limburgica* (probably Alportian), *Stygne roemeri* (probable early Kinderscoutian), *Brodioptera stricklani* (probable Kinderscoutian), and *Protoprosbole straeleni* (probable early Marsdenian). This is mainly caused by the now less reliable old datings and by the impossibility of stratigraphical correlations over long distances as from North and South America to Europe. Exact and unequivocal age determinations are only available for *Delitzschala bitterfeldensis*, the first known Arnsbergian (= Lower Carboniferous) insect, for both *Patteiskya bouckaerti* and *Schmidtopteron adictyon* from the middlepart of the Marsdenian (R2b2) as well as for the rich insect fauna from Hagen-Vorhalle which is of higher Marsdenian (R2c1) age.

The three species from the Malanzán Formation in the Paganzo Basin, Argentina, can most likely be excluded from the Namurian and placed in the early Westphalian.

4. ACKNOWLEDGEMENTS

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