A NEW FOSSIL DRAGONFLY FROM THE UPPER JURASSIC IN GERMANY [ODONATA, ANISOPTERA, PROTOLINDENIIDAE]

BY

André NEL*, Günter BECHLY**, and Xavier MARTINEZ-DELCLOS***

*Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, F–75005 Paris, France. fax : 01 40 79 36 99, e-mail: anel@mnhn.fr

**Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie, Rosenstein 1, D-70191 Stuttgart, Germany, e-mail: bechly.smns@naturkundemuseum-bw.de

***Departament Geologia Dinàmica, Geofísica i Paleontologia, Facultat de Geologia, Universitat de Barcelona, E–08071, Barcelona, Spain, e-mail: delclos@geo.ub.es

RÉSUMÉ

Une nouvelle espèce de Protolindeniidae (Odonata: Anisoptera), Protolindenia viohli *n. sp., est décrite des calcaires lithographiques du Jurassique supérieur de la Bavière (Allemagne).*

Key words: Odonata, Petalurida, Protolindeniidae, *Protolindenia viohli* sp. n., Upper Jurassic, Solnhofen, Germany.

Our knowledge about the Mesozoic Odonata Anisoptera has greatly increased during the last years with the discovery of numerous new taxa (NEL *et al.,* 1993; NEL *et al.*, 1998; BECHLY *et al.*, 2001; and others). Nevertheless, numerous further new taxa remain to be described, from old collections as well as from recent discoveries. We here describe a well-preserved specimen of *Protolindenia* corresponding to a new species from the Upper Jurassic of Germany.

In the following study we use the wing venation nomenclature of RIEK (1976) and RIEK & KUKALOVÁ-PECK (1984), amended by KUKALOVÁ-PECK (1991), NEL *et al.* (1993) and BECHLY (1996). We follow the phylogenetic classification of Anisoptera proposed by BECHLY (1996).

Genus *Protolindenia* Deichmüller, 1886

Type-species. *Protolindenia wittei* (Giebel, 1860).

Further species. *Protolindenia viohli* sp. n. The two species *Protolindenia deichmuelleri* and *P. aktassica,* both described by PRITYKINA (1968), have been transferred to the genera *Pritykiniella* and *Kazakhophlebia* respectively by NEL *et al.* (1998), and placed in Anisoptera *incertae sedis*.

Amended diagnosis. NEL *et al.* (1998) proposed a new diagnosis of the genus *Protolindenia*. We amend it below to include the new species *P. viohli*. Wings between 41 to 52 mm long; a oblique pterostigmal brace cross-vein present (at least in the forewing) and basally recessed well basal of pterostigma; area between costal margin and RA, distal of pterostigma elongate and with many cross-veins; forewing discoidal triangle not transverse but nevertheless broad; hindwing discoidal triangle longitudinal elongate and two- or three-celled; well-defined subdiscoidal triangles in all wings, those of forewings being one- or three-celled, but those of hindwings unicellular; anal loop usually posteriorly open and small (divided into 3-4 cells); veins Rspl and Mspl very poorly defined and strongly zigzagged; two lestine oblique cross-veins 'O'; two primary antenodal cross-veins stronger than the secondary antenodal cross-veins, separated by two or four secondaries; arculus closer to Ax1 than Ax2; Ax2 slightly basal or nearly opposite distal angle of discoidal triangle; primary IR1 very long, more or less straight, and originating well basal of pterostigma, below or basal pterostigmal brace vein; pseudo-IR1 well defined; MA and RP3/4 closely parallel and undulated near posterior margin; IR2 and RP2 relatively straight and closely parallel, area between them being narrowed distally; CuA divided into 5-7 parallel posterior branches; distinct pseudo-anal vein PsA present in forewing; wings hyaline; female abdomen rather thick; male anal appendages not foliate; compound eyes distinctly separated.

Protolindenia viohli sp. n.

(Figs 1-4)

Material. Holotype specimen MNHN-LP-R.55239 (imprint and counterimprint) (coll. Nel), Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France, paratype specimen SOS 1693 Jura-Museum.

Stratum typicum. Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, Hybonotum-Zone, Solnhofen Lithographic Limestone.

Locus typicus. Solnhofen, southern Frankonian Alb, Bavaria, Germany.

Derivatio nominis. Named in honour of Dr Günter Viohl, the director of the Jura-Museum in Eichstätt (Germany).

Diagnosis. This new species is distinguished from *P. wittei* by the following characters: wings shorter than those of *P. wittei* (41.6 to 44 mm compared to 41 to 52 mm long); hindwing pterostigmal brace completely reduced; forewing pterostigmal brace only one cell basal of pterostigma and not oblique; forewing subdiscoidal triangle unicellular, instead of being three-celled in *P. wittei*; the anal loop seems to be posteriorly better closed, even though this last character is rather variable in *P. wittei*.

Description.

Holotype. Imprint of a nearly complete specimen, with one hindwing missing. The wings are well preserved and hyaline.

Forewing 44.0 mm long, 9.7 mm wide; ratio width/length, 0.22; distance from base to nodus, 22.8 mm; from nodus to apex, 21.2 mm; from nodus to pterostigma, 12.0 mm; from pterostigma to apex, 5.0 mm; from nodus to arculus, 16.6 mm; pterostigma 5.1 mm long, 0.8 mm wide and rather narrow, with about six cells below it; pterostigmal brace vein not oblique, stronger than postnodal cross-veins, and situated 1.0 mm (one cell) basal of pterostigma; about fourteen postnodal cross-veins, not strictly aligned with corresponding postsubnodal cross-veins; 16 secondary antenodal cross-veins; antenodal cross-veins of second row, between ScP and RA, less numerous and not aligned with those of first row; 2 strong primary antenodal cross-veins with 4 secondaries between them. Ax1 1.3 mm basal of arculus; distance between Ax1 and Ax2, 5.6 mm; Ax2 being slightly basal of distal angle of discoidal triangle; RP and MA well separated in arculus; arculus not distinctly angled; numerous cross-veins between RP and RA basal of RP3/4 and between base of RP3/4 and nodus; numerous cross-veins between RP and MA basal ofRP3/4; 7 bridge-cross-veins (Bqs); discoidal triangle two- or three-celled, not elongate and narrow; length of its anterior side, 3.2 mm; of distal side, 3.5 mm; of basal side, 2.3 mm; anterior side of discoidal triangle joining MAb;

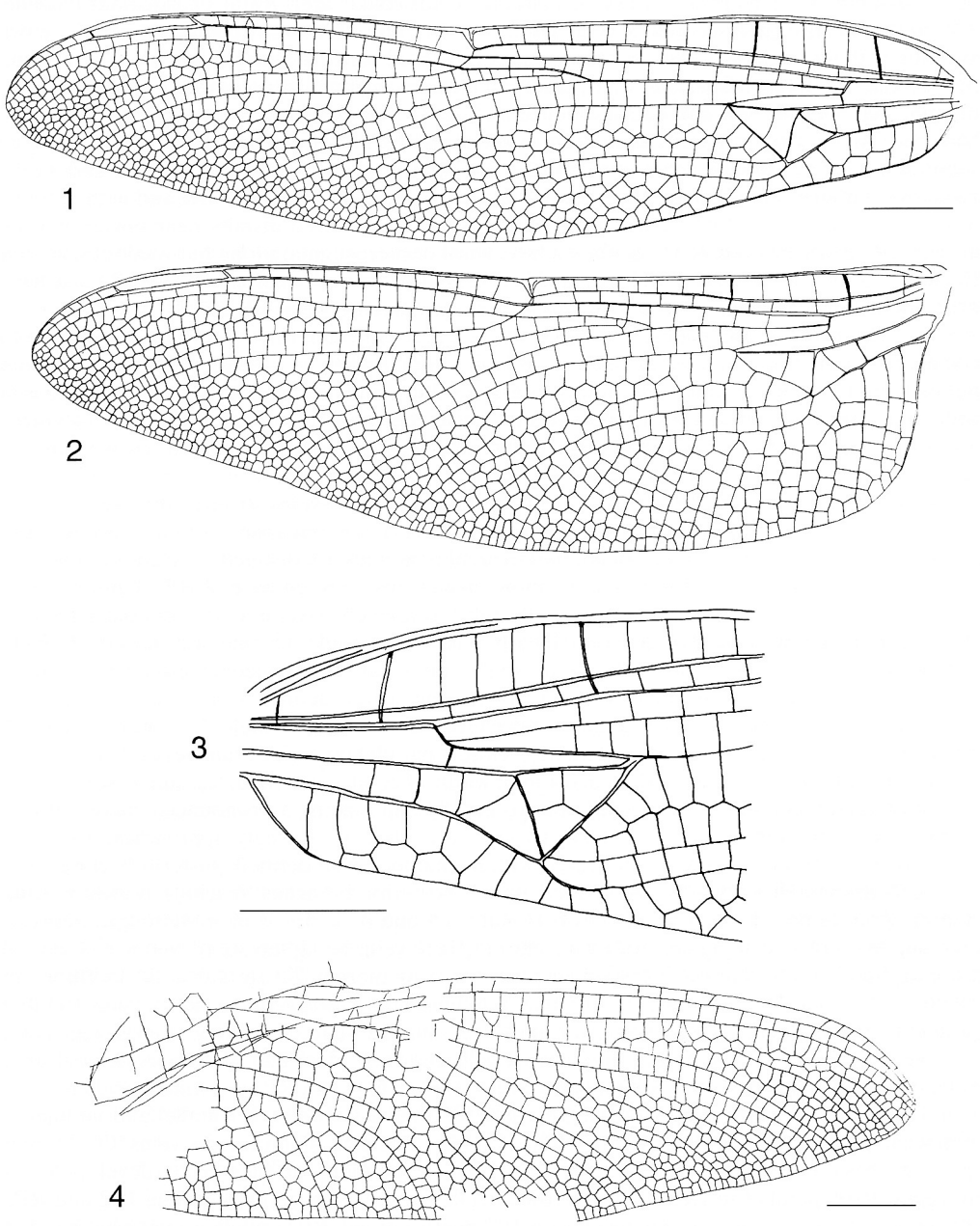

Fig. 1-4, ***Protolindenia viohli*** sp. n. — 1-3, holotype specimen MNHN-LP-R.55239: left forewing (1), left hindwing (2), base of right forewing (3). — 4, paratype specimen SOS 1693, right hindwing. Scale bar represents 4 mm.

supratriangle and median cell free of cross-veins; submedian cell traversed by CuP-crossing and by 2 supplementary cubito-anal cross-veins, one basal of CuP and the other between CuP and PsA; a well-defined PsA separating submedian cell from a nearly triangular unicellular subdiscoidal triangle, the latter being 2.5 mm long and 1.8 mm wide; 2 rows of cells in anal area; CuA divided into 5-6 posterior branches, comparatively long and reaching posterior wing margin slightly basal of nodus; 5-7 rows of cells between CuA and posterior wing margin; area between CuA and MP widened near posterior wing margin with one row of cells behind discoidal triangle and 12 rows

near posterior wing margin; 3 rows of cells in postdiscoidal area distal of discoidal triangle; 2 longitudinal zigzagged secondary veins parallel to MP and MA in postdiscoidal area; the more anterior of these secondary veins continuing as a zigzagged concave vein (rudimentary Mspl); one row of cells between Mspl and MA; postdiscoidal area widened distally along posterior wing margin; area between MA and RP3/4 widened and with 4 rows of cells near posterior wing margin; MA and RP3/4 closely parallel, and somewhat distal of nodus, undulate; RP2 originating at subnodus; 2 lestine oblique cross-veins 'O', 2.4 mm apart; the basal one being 1.6 mm and 3 cells distal of subnodus; an indistinctly developed and zigzagged Rspl, parallel to IR2 and with one row of cells between it and IR2; area between IR2 and RP2 narrowed distally near posterior wing margin; IR2 gently curved. RP2 undulate a little basal of pterostigma; a long but weakly zigzagged IR1 starting somewhat basal of pterostigmal brace; 3-4 rows of cells in area between IR1 and RP2; 4-5 rows of cells and one secondary longitudinal vein in area between IR1 and RP1.

Hindwing 41.6 mm long, 12.3 mm wide, 12.2 mm wide under nodus; distance from base to nodus, 18.8 mm; from nodus to apex, 22.8 mm; from nodus to pterostigma,13.5 mm; from pterostigma to apex, 4.7 mm; from nodus to arculus, 13.3 mm; pterostigma 5.2 mm long, 0.8 mm wide and rather narrow; pterostigma covering 4 cells; no distinct pterostigmal brace; 14 visible postnodal cross-veins, not strictly aligned with corresponding postsubnodal cross-veins; 11 secondary antenodal cross-veins, not strictly aligned with corresponding antenodal cross-veins of the second row between ScP and RA; 2 primary antenodal cross-veins stronger than secondaries, with 3 secondaries between them; arculus very near to Ax1, 0.8 mm apart; distance between Ax1 and Ax2, 5.2 mm; RP and MA well-separated in arculus; arculus not distinctly angled; 4 cross-veins between RP and RA basal of RP3/4 and 4 more cross-veins between base of RP3/4 and nodus; 6 cross-veins between RP and MA basal of RP3/4; 5 bridge-cross-veins (Bqs); discoidal triangle elongate and narrow, crossed by one vein; length of its anterior side, 3.5 mm; of distal side, 3.8 mm; of basal side, 1.9 mm; distal side with a weak angle; supratriangle and median space free of cross-veins; submedian space only traversed by CuP-crossing; a well-defined vein PsA separating the submedian space from a nearly triangular unicellular subdiscoidal triangle, 1.7 mm long and 1.6 mm wide; no anal triangle, thus it is a female; 2 closely parallel posterior branches of AA; 6-7 rows of cells in anal area; width of anal area, 6.4 mm; width of cubito-anal area, 5.2 mm; first posterior branch of CuAb well-defined, directed postero-basally and making a pronounced curve towards posterior wing margin; CuAb very distinctly curved at its base, strongly approaching the most distal posterior branch of AA but not fused with it; anal loop well defined, posteriorly closed and three-celled; main branch of CuA divided into 7 posterior branches, reaching posterior wing margin opposite nodus; 6-7 rows of cells between CuA and posterior wing margin; area between CuA and MP widened along posterior wing margin, these veins being separated by one row of cells distal of discoidal triangle and 8 rows near posterior wing margin; 2-3 rows of cells developed in postdiscoidal area distal of discoidal triangle; 2 longitudinal zigzagged secondary veins running parallel to MP and MA, the more anterior of these secondary veins continuing as a zigzagged and concave vein (rudimentary Mspl); one row of cells between Mspl and MA; postdiscoidal area widened distally near posterior wing margin; area between MA and RP3/4 distinctly widened and with 3 rows of cells along posterior wing margin; MA and RP3/4 closely parallel and undulated somewhat distal of nodus; RP2 aligned with subnodus; 2 lestine oblique cross-veins 'O', 3.9 mm apart; the basal one being 1.4 mm and 2 cells distal of subnodus; an indistinctly developed and zigzagged Rspl, parallel to IR2, with one row of cells between them; area between IR2 and RP2 narrowed distally near posterior wing margin; IR2 gently curved; RP2 undulate somewhat basal of pterostigma; primary IR1 long, zigzagged and beginning 6 cells basal of pterostigmal brace; 3 rows of cells between IR1 and RP2; 4-5 rows of cells and one secondary longitudinal vein in area between IR1 and RP1; pseudo-IR1 well defined.

Head poorly preserved; thorax about 10.0 mm long; abdomen 47.0 mm long, 4.5 mm wide; cerci simple without spines, 5.0 mm long and 0.5 mm wide; ovipositor clearly visible, 6.0 mm long but not extending beyond cerci.

Paratype SOS 1693. Only the distal two third of a hindwing preserved; no trace of coloration; width of the wing, 11.0 mm; distance from nodus to pterostigma, 12.3 mm; from nodus to apex, 22.0 mm; from pterostigma to apex, 5.3 mm; pterostigma 5.6 mm long and 0.6 mm wide; except for its smaller dimensions, all the preserved wing structures agree with those of the hindwing of the holotype.

Discussion. *Protolindenia viohli* sp. n. has the main autapomorphies of the Petalurida (NEL *et al.*, 1998): postnodal space very narrow, with many cells distal of pterostigma; stigmal brace shifted basally, about midway between node and apex; primary IR1 well-defined, rather straight, and very long in both wing pairs; wing space between RP1 and RP2 (especially in forewings) strongly expanded, with much more than 8-9 rows of cells; forewing pseudo-anal vein PsA hypertrophied and subdiscoidal triangle widened; in both wing pairs more than 2 rows of cells in basal part of postdiscoidal area between level of distal angle of discoidal triangle and that of midfork; in hindwings, CuAb distinctly curved at its base, strongly approaching the most distal posterior branch of AA.

The only difference to the other known Petalurida is its forewing subdiscoidal triangle being unicellular and not divided by cross-veins.

NEL *et al.* (1998) only proposed a single wing-venational synapomorphy for the family Protolindeniidae, i.e. the complete reduction of the anal loop. This is a very weak character, since it is convergently present in Aktassiidae, *Phenes* and Petalurinae, as well as in many other Anisoptera. It is not shared by *P. viohli*. Nevertheless, the wing venation of *P. viohli* is strikingly similar to that of *P. wittei*, the main differences being listed in the diagnosis of the new species. Therefore, we attribute this new species to the genus *Protolindenia*.

With the present discovery, the dragonfly fauna of the lithographic limestone from Bavaria includes about 18-20 families and 52 species, of which several species probably are of dubious taxonomic status, while some others are not yet scientifically described. Anyway, the Solnhofen limestones yielded one of the most diverse fossil odonate faunas known at all, maybe only matched by the Lower Cretaceous Crato limestones from Brazil.

REFERENCES

BECHLY (G.), 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der phylogenetischen Systematik und des Grundplanes der *Odonata. *Petalura*, Böblingen, Special Volume 2: 402 p.

BECHLY (G.), NEL (A.), MARTÍNEZ-DELCLÒS (X.), JARZEMBOWSKI (E.A.), CORAM (R.), MARTILL (D.), FLECK (G.), ESCUILLIÉ (F.), WISSHAK (M.M.) & MAISCH (M.), 2001. A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). *Neue Paläontologische Abhandlungen* 4: 219 p.

KUKALOVÁ-PECK (J.), 1991. Chapter 6: Fossil history and the evolution of hexapod structures. pp. 141-179. *In*: NAUMANN (I.D.) [Ed.]. *The insects of Australia, a textbook for students and research workers* (2nd ed.), 1, (Melbourne University Press, Melbourne): 542 p.

NEL (A.), BECHLY (G.), MARTÍNEZ-DELCLÒS (X.) & JARZEMBOWSKI (E.A.), 1998. A new revision of the Recent and fossil Petaluridae (Insecta, Odonata, Anisoptera). *Paleontologia lombarda* (N.S.) 10: 1-68.

NEL (A.), MARTÍNEZ–DELCLÒS (X.), PAICHELER (J.–C.) & HENROTAY (M.), 1993. Les "Anisozygoptera" fossiles. Phylogénie et classification. (Odonata). *Martinia*, Bois d'Arcy, numéro hors série 3: 1–311.

PRITYKINA (L.N.), 1968. Strekozy Karatau (Odonata) [Dragonflies from Karatau (Odonata), p. 26-55. *In*: Panfilov, D.V. [Coord.], *Yurskie Nasekomye Karatau*. [Fossil insects from Karatau]. Academy of Sciences of the S.S.S.R., Nauka, Moscow: 252 p. [in Russian.]

RIEK (E.F.), 1976. A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum,* Pietermaritzburg, 22 (3): 791-820.

RIEK (F.) & KUKALOVÁ–PECK (J.), 1984. A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology* 62: 1150–1166.