SURFACE LASER SCANNING OF FOSSIL INSECT WINGS

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ABSTRACT. Primary homologization of wing venation is of crucial importance in taxonomic studies of fossil and recent insects, with implications for large-scale phylogenies. Homologization is usually based on relative relief of veins (with an insect ground plan of alternating concave and convex vein sectors). However, this method has led to divergent interpretations, notably because vein relief can be attenuated in fossil material or because wings were originally flat. In order to interpret better vein relief in fossil insect wings, we tested the application of non-contact laser scanning. This method enables high resolution three-dimensional (3-D) data visualization of a surface, and produces high quality images of fossil insect wings. These images facilitate and improve interpretation of the homologization of wing venation. In addition, because the surface information is digitised in three axes (X, Y, Z), the data may be processed for a wide range of surface characteristics, and may be easily and widely distributed electronically. Finally, this method permits users to reconstruct accurately the fossils and opens the field of biomechanical interpretation using numerical modelling methods.

KEY WORDS: laser scanning, insect, wing venation pattern, digitization, 3-D.

BECAUSE wings are usually the best-preserved structures in fossil insects, the primary homologization of wing veins has become crucial in studies of fossil insect taxa. This homologization is usually achieved through the determination of pairs of convex (= located on an elevation) anterior and concave (= located in a depression) posterior sectors of main veins (Redtenbacher 1886; Brongniart 1893; Laurentiaux 1953; Kukalová-Peck 1983, 1991; Carpenter 1992).

This important information is often difficult to observe on fossils, and is usually only described qualitatively. This lack of explicit quantitative data leads to controversies in interpretation of wing venations (e.g. for Orthoptera: Rasnitsyn 1980; Kukalová-Peck 1991; Carpenter 1992; Béthoux and Nel 2002), and consequent incongruities in proposed insect phylogenies. These controversies may be resolved if representation and measurements of vein relief can be achieved.

In order to obtain such measurements, we explored the use of a 3-D non-contact surface profiler. This method yields a 3-D data set of the fossil surface, which can be used to image the surface and to process it for detailed investigation. Numerous 3-D restorations have been attempted on fossil material (mainly vertebrate remains), some of them using laser technology (Lyons *et al.* 2000). Here we report on 3-D laser scanning, with the highest available resolution, of fossil insect wings.

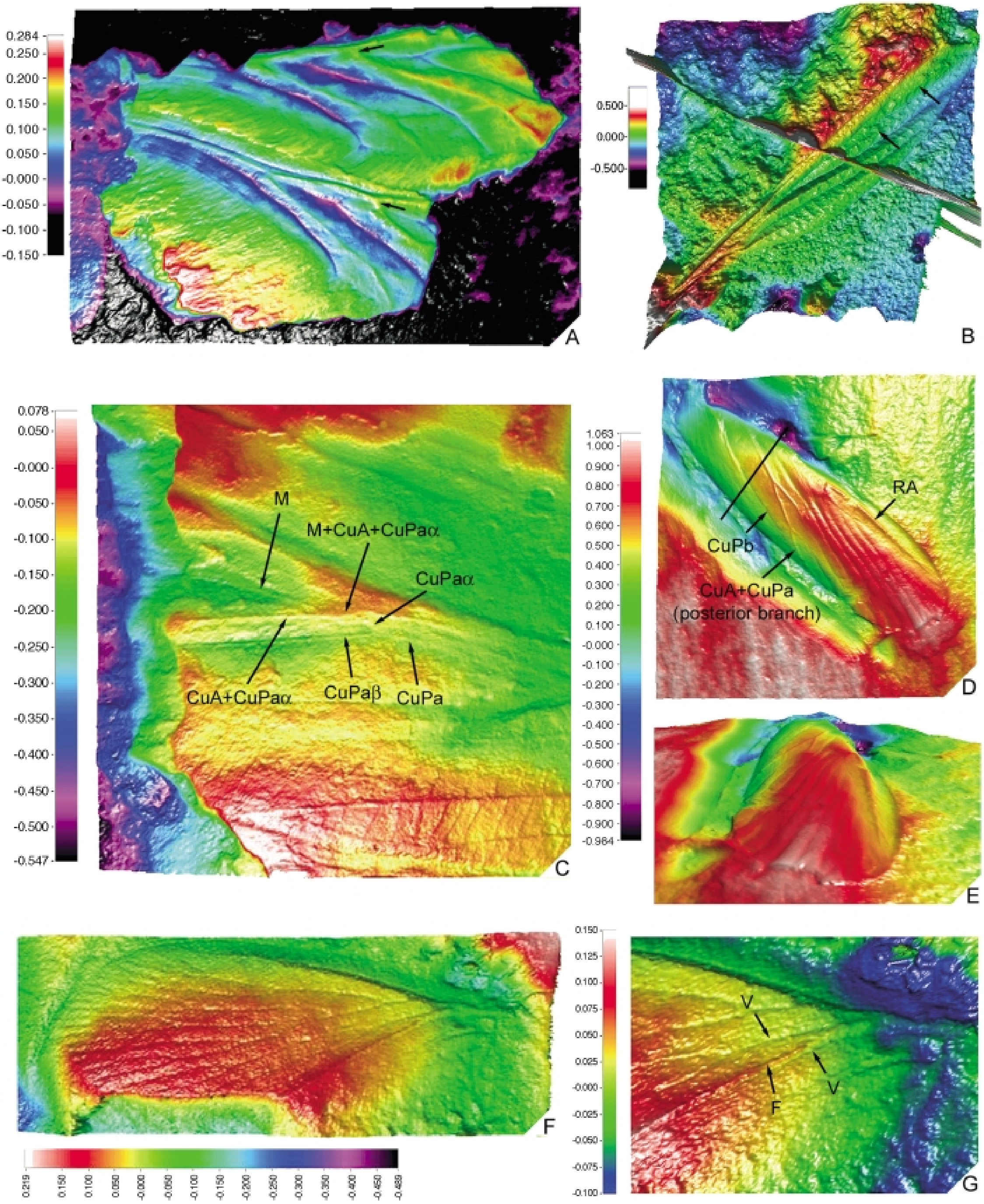
MATERIAL AND METHODS

Fossils

The fossils examined were: *Ischnoptilus elegans* Brongniart, 1893 [holotype specimen MNHN-LP-R.51288, Muséum national d'Histoire naturelle (MNHN), Paris, France; Palaeoptera, Megasecoptera; Upper Carboniferous; Commentry Basin, France]; *Epilestes gallica* Nel *et al.*, 1999 (holotype specimen Ld LAP 110, Musée Fleury, Lodève, France; Palaeoptera, Odonatoptera; Upper Permian; Lodève Basin, France); *Caloneura dawsoni* Brongniart, 1885 (specimen MNHN-LP-R.51356, MNHN as above; Neoptera, Caloneurodea; Upper Carboniferous; Commentry Basin, France); an undescribed Tococladidae (specimen Ld LAP 308a, Musée Fleury as above; Neoptera, Archaeorthoptera; Upper Permian; Lodève

Basin, France); an undescribed Neoptera, Endopterygota (Roques and Nel, pers. comm. 2002) (specimen MNHN-LP-R.55181, MNHN as above; Upper Carboniferous; Pas-de-Calais, France).

Fossil insect wings, preserved as compressions, that appeared to retain natural relief were chosen. This selection was made after considering all specimens (for *Caloneura* and the undescribed Tococladidae),



and after comparison with other specimens belonging to closely related taxa (for *Ischnoptilus*, *Epilestes* and the undescribed Endopterygota) and with closely related extant taxa.

In the following study we follow the insect wing venation nomenclature of Kukalová-Peck (1991) and Béthoux and Nel (2002) (as elaborated for Archaeorthoptera, and derived from the general scheme of Kukalová-Peck, 1991): R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPaα, anterior branch of CuPa; CuPaβ, posterior branch of CuPa; CuPb, posterior branch of CuP.

Measurements

The measurements were made at TaiCaan Technologies Ltd (Southampton, UK). Two systems were used in the study: the Xyris 3000 and the Xyris 4000LT (see www.taicaan.com for system details). The 3000 system (used to collect the data shown in Text-fig. 1A–E) uses a laser triangulation probe with a laser spot size of 30 μm that is scanned across the fossil surface at high speed, typically 1–2 minutes for the data shown in the figures. The illustrations in Text-fig. 1F–G were obtained from the use of a confocal laser (4000LT) with a spot size of 2 μm. With this system the laser light is always focused on the surface resulting in increased measurement precision. The images shown are generated from the data using 'TaiCaan Viewer 2002' software. The data sets can be rotated and the lighting and colour rendering changed. The data can also be used to process the surface for a wide range of parameters, such as surface area and surface roughness, via a two-dimensional cross section through the wing structure (Text-fig. 2).

RESULTS

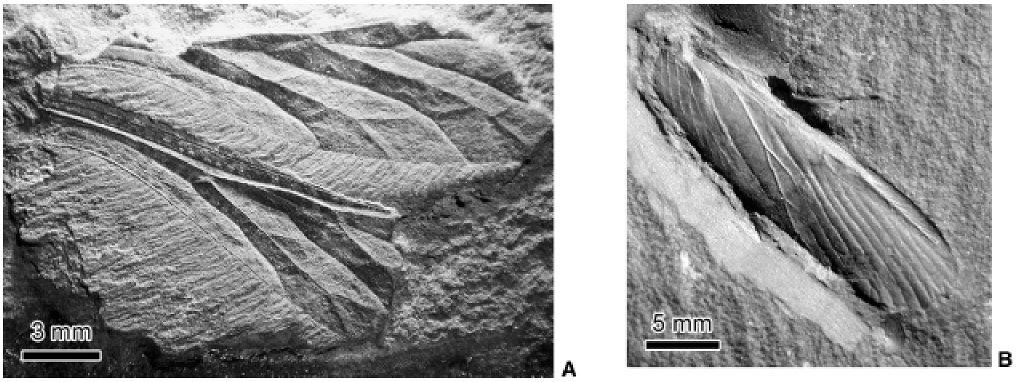
The non-contact surface scanning method described provides efficient measurements of surface relief regardless of the sediments tested. In a few confined points, the triangulation laser was inefficient because of the orientation of some reflecting minerals. Obviously, colouration due to organic matter (in the case of the Commentry fossils) is not registered. Importantly, the laser beam does not destroy the organic matter.

The surface profiler using a laser triangulation probe has a lateral resolution (30 μm) that is convenient at our observation level, but magnifications are limited. The diverse fossils tested demonstrate the adequacy of the tool used for the required purpose.

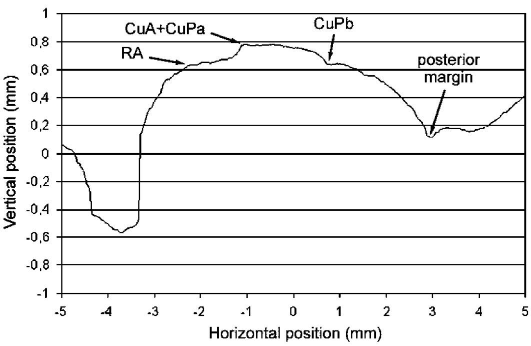
Because the layer containing *Ischnoptilus* is isolated and located on an upper level of the specimen, the scale has been shifted in order to make measurements of wing relief more acute. The laser scan of *Ischnoptilus* shows an alternation of convex (red to green) and concave (purple to blue) veins (Text-fig. 1A), well marked on these Palaeozoic Palaeoptera (Text-fig. 2A). This primitive alternation is currently used for homologization of venation: convex veins are anterior sectors, concave veins are posterior sectors (in situations without modification of vein relief). Additionally, refinements of wing venation of *Ischnoptilus*, such as strong convex struts between RA and RP, are clearly visible.

In the case of the *Epilestes*, the available specimen is a counterpart. Thus the laser scan has been mirrored in order to show the relief of the dorsal veins (Text-fig. 1B). The relief of the distal part of the

TEXT-FIG. 1. All scales in mm. A, *Ischnoptilus elegans*: 3-D restoration of the right wings and a part of the body; illustration of the primitive alternation of convex (red to green) and concave (purple to blue) sectors; arrows indicate convex struts; surface scanned: 24·0 × 16·0 mm. B, *Epilestes gallica*: 3-D restoration of the wing (reversed because the specimen is a counterpart); vertical dimension magnified (×4·4); arrows indicate supplementary concave branches, between concave branches of RP; surface scanned: 24·5 × 24·5 mm. C, *Caloneura dawsoni*: 3-D restoration of the base of the fore-wing; 'panorthopterid' interpretation of the venation after veins relief of the medio-cubital area; surface scanned: 12·0 × 12·0 mm. D, undescribed Tococladidae: 3-D restoration of fore-wing; RA (convex) and the posterior branch of CuA + CuPa (convex) delimit the distal deformable area; bar indicates location of profile illustrated in Text-figure 3; surface scanned: 24·0 × 24·0 mm. E, undescribed Tococladidae: 3-D restoration of fore-wing, view from apex to base. F, undescribed Neoptera: Endopterygota (specimen MNHN-LP-R.55181): 3-D restoration of hind-wing; surface scanned: 21·0 × 6·0 mm. G, as for F: magnification of the base of hind-wing; V, vein; F, fold.



TEXT-FIG. 2. A, *Ischnoptilus elegans*: traditional photograph of the right wings and a part of the body. B, undescribed Tococladidae: photograph of fore-wing.



TEXT-FIG. 3. Undescribed Tococladidae: cross-section of the fore-wing as indicated on Text-figure 1D.

wing is not very marked; thus we have magnified the vertical dimension (× 4·4). In the posterior Radius area, an alternation of concave and convex veins occurs. The concave veins are true branches of RP and the convex veins are supplementary intercalary veins (arrows on Text-fig. 1B), present in Odonatoptera wings. They are easily recognizable through this analysis.

Analysis using the new technique illustrates that the wing base of *Caloneura* has a venation pattern more complex than expected. There is a short concave branch (CuPaα) that emerges from a concave vein (CuPa) and fuses with a strongly convex vein (M + CuA). A concave vein (M) and a convex vein (CuA + CuPaα) emerge from this composite vein [(M + CuA) + CuPaα] (Text-fig. 1C; vein names after Béthoux and Nel 2002).

The dorsal cambering of the forewing in the undescribed Tococladidae is illustrated in Text-figures 1D–E and 3, and is difficult to appreciate from the photograph (Text-fig. 2B). A distal area is characterized by a series of simple, slender and parallel veins, with a uniform neutral relief. This area is delimited by two convex veins: the 'Radius Anterior' (RA) and the posterior branch of CuA + CuPa. The area between posterior branch of CuA + CuPa and CuPb is slightly dorsally cambered (Text-fig. 3). These features and their biomechanical implications will be discussed in detail elsewhere.

The 'surface profiler with confocal laser' method was tested on the undescribed Endopterygota. The strongly convex fold visible on this wing, difficult to identify because of confusion with a true vein, is clearly visible in this image (Text-fig. 1F–G). These illustrations support the interpretation that this structure is a fold, because unlike true veins it has an unclear origin. The confocal laser enables fine plotting for studies of very delicate structures. Its lateral resolution (2 μm) is usually less than the grain-size of the sediment, and provides a record of the all of the relief information present on the fossil. However, its use on large surfaces requires a customized system, not available for our tests.

DISCUSSION

Observation, illustration and interpretation of fossil insect wings

The observation of fossil insect wings is improved by the use of surface laser scanning, notably after magnification of the original relief. This technique also helps in the interpretation of confusing structures. Illustration of fossil insect wings using this method compensates for certain deficiencies of traditional photography: features very difficult to illustrate, such as wing cambering, can be clearly illustrated and easily measured. When applied to fossils with pronounced relief, such as *Ischnoptilus*, the laser scan does not have the problem of over-emphasized contrast which is unavoidable using traditional photography. Additionally, the new method overcomes limitations owing to depth of field of objectives and provides explanatory views that were not possible previously (Text-fig. 1E). Also, this method of illustration permits greater appreciation of the quality of preservation and hence the limits of interpretation.

Several interpretations of the wing venation of Caloneurodea are available in the literature. That of Rohdendorf (1962) implies a reversal of the relief of some veins, with a convex MP and a concave CuA, which is a non-parsimonious hypothesis. That of Rasnitsyn (1980) implies the presence of a strongly convex posterior branch of M (Russian 'M5'), and a reversal of the relief of CuA (concave instead of convex), which is also a non-parsimonious hypothesis. Those of Kukalová-Peck (1991) and Carpenter (1992) are consistent with the relief of veins (they only differ in the interpretation of the branching of M), but both ignore the occurrence of the short concave anterior branch of CuPa. Finally, the 'panorthopterid' interpretation (see above; Béthoux and Nel 2002) is supported by current measurements. Consequent phylogenetic implications are important: the order Caloneurodea must, therefore, be considered as sister-group related to the Orthoptera, rather than related to Cimiciformes (= Paraneoptera + fossil orders; Rasnitsyn 1980), hemipteroid insects (Kukalová-Peck 1991) or Protorthoptera (Carpenter, 1992). This example underlines the importance of laser scanning for interpretation of venation and proposing phylogenetic hypotheses.

Digitization, curation and electronic distribution

The application of surface laser scanning of fossil insect wings (preserved as compressions) leads to digitization of all relief information present (notably with the confocal laser). Digitization is the best way for recording this information, and also for making it accessible. If this method becomes widely used, the creation of a freely accessible database that provides reliability, authenticity and perpetuation of electronic records (Duranti 2001) would ensure distribution of the information. Moreover, on the basis of three-dimensional data, models could be accurately produced via rapid prototyping technology such as stereo-lithography (see http://home.att.net/~castleisland/sla_int.htm). This technique would allow easy reproduction of fossils and enrich museum collections and exhibitions.

Data recording is also important when potentially destructive mechanical preparation is needed, e.g. when a number of wings are overlapped and partly hidden. The overlapping part can be removed after recording its relief (traditional photography can be coupled with this method when it is considered beneficial to record colour information).

Biomechanical studies

Information on the pattern of venation, vein relief, thickness, and wing cambering are important for qualitative interpretations of the biomechanical behaviour of insect wings during flight (Ennos 1988; Wootton 1992; Brodsky 1994; Dudley 2000; Gorb 2000; Wootton *et al.* 2000). However, digitization of a fossil wing included in a three-dimensional restoration of the whole insect could permit quantification of its flight performances via modelling approaches (Herbert *et al.* 2000). A potential problem involves assessing the degree of compression of the fossil, although potentially this can be estimated by considering closely related extant representatives or levels of compression of other fossils from the same locality (e.g. specimens of the still extant *Triops cancriformis* have been recorded from the Permian of the Lodève Basin, and have a relief that is very similar to that of modern material; Gand *et al.* 1997). Parameters unobtainable from the fossil record, such as wing thickness, occurrence of resilin-type joints (Gorb 2000), stroke angle, and phase shifts between fore- and hind-wings, might be assessed from extant taxa and tested on fossil taxa using computerized models. Such studies will improve our knowledge of the origin and evolution of insect flight and its ecological significance.

CONCLUSION

The use of surface laser scanning provides reliable data on the relief of fossil insect wings. Wider use of this method may increase the quality of palaeoentomological studies, in improving observation, illustration and interpretation of the fossils. Furthermore, this technique guarantees the preservation and wide distribution of the information. It may also become a preliminary but necessary step in reconstructing the flight of fossil insects. Because of these crucial applications this tool is likely to become an essential requirement for palaeoentomological laboratories.

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