A NEW THREE-DIMENSIONALLY PRESERVED XIPHOSURAN CHELICERATE FROM THE MONTCEAU-LES-MINES LAGERSTÄTTE (CARBONIFEROUS, FRANCE)

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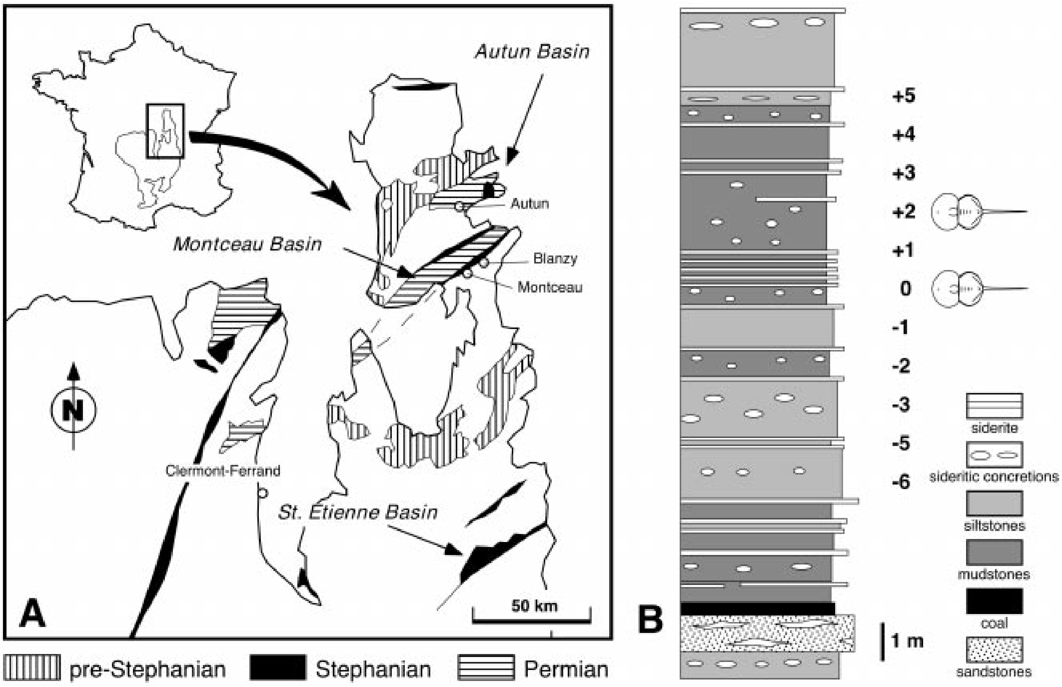
ABSTRACT. Excellent three dimensional preservation of 142 specimens of *Alanops magnificus* gen. et sp. nov. (Chelicerata: Xiphosura) from the Stephanian Konservat-Lagerstätte of Montceau-les-Mines (Saône-et-Loire, France), exposes the carapace design and hitherto unrecorded details of fossil xiphosuran ventral anatomy, and makes possible an interpretation of appendicular functional morphology. All legs are long, slender and chelate. The chelate condition of the fifth leg and the shape of the prosoma (highly vaulted with a subvertical frontal area) indicate that the animal was neither a burrower like Recent xiphosurans (e.g. *Limulus*) nor an active swimmer as suggested for other extinct forms, but was more likely to have been a benthic crawler. The ability to fold up is attested by both partly enrolled specimens showing appendages withdrawn into the prosomal cavity, and by coaptive devices on the external and internal margins of both prosoma and opisthosoma. The low-level articulation system at the boundary between the two shields allowed both the carapace closure and the complete outstretching of the animal. The unusually small adult size of *Alanops magnificus* gen. et sp. nov. combined with the loss of ophthalmic ridges and spines is interpreted as indicating a paedomorphic derivation from a bellinurine stock. The depositional environment (limnic intramontane basin) and faunal association (dominated by syncarids and bivalves) of *Alanops* indicate that the animal probably lived in fresh water.

KEY WORDS: Chelicerata, Xiphosura, Konservat-Lagerstätte, Montceau-les-Mines, Carboniferous.

RECENT xiphosurans are conventionally regarded as archetypes of 'living fossils' (Fisher, 1984). This assumption is based on comparisons between fossil xiphosurans (Mesozoic and Palaeozoic) and living limulid species (Schuster 1982), and relies chiefly on superficial resemblances (dorsal exoskeleton), or indirect evidence from the study of trace fossils (Goldring and Seilacher 1971; Barthel 1974). To date, *Weinbergina* from the Devonian Hunsrück Slate of Germany (Stürmer and Bergström 1981), *Euproops* from the Carboniferous of England (Anderson 1996), and *Paleolimulus* from the Permian of Kansas (Dunbar 1923), are among the few Palaeozoic xiphosurans that exhibit details of their ventral anatomy. However, the material is either flattened, pyritized, or tectonically distorted. We describe here uncompacted specimens of a xiphosurid found in the sideritic concretions of the Stephanian B–C (Babin 1994; Doubinger 1994; Langiaux 1994) Konservat-Lagerstätte of Montceau-les-Mines (Saône-et-Loire, France; see Text-fig. 1). Although xiphosurid representatives were not rare during the Carboniferous, and occur virtually world-wide, the material described here is unique in two major aspects: (1) the exquisite 3-D preservation of ventral and dorsal exoskeletal features including complete appendages and (2) the numerical abundance of both juveniles and adults that allows the study of biometrics and ontogeny of a fossil xiphosuran for the first time. *Alanops magnificus* gen. et sp. nov. is the only xiphosuran species of the Montceau-les-Mines biota. This low diversity contrasts with that of other localities which commonly yield several representatives of the group (Anderson *et al*. 1997). For example, the Mazon Creek Konservat-Lagerstätte (Westphalian D equivalent, USA; see Mikulic 1997) contains up to five genera and species, although it is not always established whether they actually co-occur at the same level.



TEXT-FIG. 1. Location and stratigraphic position of the fossiliferous concretion-bearing layers. A, map of the north-eastern part of the Massif Central with the main Carboniferous and Permian basins (modified after Poplin 1994, fig. 3). B, lithological succession in the Saint-Louis opencast pit. Fossiliferous concretion-bearing beds are numbered −6 to +5; those yielding *Alanops magnificus* gen. et sp. nov. are 0 and +2 (after Pacaud and Sotty, fig. 1 *in* Heyler and Poplin 1994).

BACKGROUND OF THE MONTCEAU-LES-MINES LAGERSTÄTTE

Geographical and stratigraphical setting

The Blanzy-Montceau-les-Mines Basin is located in the north-east part of the Massif Central (central France). It forms part of the Blanzy-Le Creusot-Bert Stephanian to Permian graben (Text-fig. 1A), which represents a major tectonic structure of Variscan trend (45–50° N) (Branchet 1983). The Stephanian deposits crop out on both sides of the graben. The Stephanian coal seams of the Blanzy-Montceau Basin crop out along the southern fringe in the vicinity of Montceau-les-Mines, where they have been extensively exploited in several opencast pits since the nineteenth century. Concretion-bearing layers were well-exposed in the Saint-Louis, Saint-François and Sainte-Hélène opencast pits, which yielded the majority of the fossil material available to date.

The concretion-bearing layers lie *c.* 40 m above the First Seam of the Assise de Montceau, and their total thickness is about 12 m. Concretions occur in clayey siltstones and silty claystones. Eleven concretion-bearing layers have been recognized (Text-fig. 1B) at the Saint-Louis pit. Xiphosurans were found in two of them (namely 0 and +2) (Pacaud and Sotty 1994; Chabard and Poplin 1999). The precise origin of a number of other specimens from the Saint-Louis pit is not specified. However they most probably originate from the same levels because no other horizon has yet yielded xiphosurans *in situ* at this locality. Other specimens originate from the Sainte-Hélène and Saint-François opencasts (Sotty *in* Chabard and Poplin 1999).

The precise age of the concretion-bearing layers within the Stephanian remains uncertain. Doubinger and Langiaux (1982) proposed a Stephanian age for the whole Carboniferous sequence of the Montceau Basin. More recently a Late Carboniferous age (Stephanian B–C–D) was deduced from plant megafossils ('assemblage 1' of Langiaux 1994) as well as from pollen and spores ('first association' of Doubinger 1994). Stephanian B is commonly accepted in the literature (Poplin and Heyler 1994) as the most probable age for the Montceau-les-Mines Konservat-Lagerstätte, but this requires confirmation. Stephanian C cannot be ruled out as it was assigned to the beds with the bivalve mollusc *Anthraconaia lusitanica* by comparison with the range of this species in Portugal (Eagar 1983; Babin *in* Poplin and Heyler 1994, p. 113). On the basis of our present state of knowledge, a Stephanian B–C age will be provisionally retained herein, but this assumption still needs to be confirmed by further refinement of zone-fossil evidence.

Faunal biodiversity

Preliminary inventories (Rolfe *in* Rolfe *et al.* 1982; Poplin *in* Poplin and Heyler 1994) gave an overview of the faunal and floral diversity of the Montceau-les-Mines biota. Although largely unpublished, more recent compositional data compiled over the last five years (Sotty *in* Chabard and Poplin 1999) from 23,250 concretions that yielded animal remains (coprolites excluded) indicate that the fauna as a whole is largely dominated by aquatic forms associated with a significant proportion of amphibian and terrestrial elements such as onychophorans, scorpions and other arachnids, myriapods (including extinct arthropleurids; Briggs and Almond 1994), insects (Rolfe *et al.* 1982) and tetrapods. Invertebrate aquatic forms are mainly crustaceans (*c*. 54 per cent of the assemblage) most of them (*c*. 91 per cent) being syncarids; other crustaceans are conchostracans (5·7 per cent), ostracods (0·08 per cent), and possibly phyllocarids and isopods. Other aquatic arthropods include the enigmatic euthycarcinoids (1·9 per cent), and xiphosurans (0·61 per cent). Bivalve molluscs (*Anthraconaia*; Babin 1994) are abundant (*c*. 26 per cent of the assemblage) but restricted in space and time to the lower part of bed 0 of the Saint-Louis pit. Other infaunal organisms include annelids as yet undescribed. Spiral coprolites are abundant and were most probably produced by fish. Their content (e.g. actinopterygian scales and teeth; Poplin 1994) gives some indication of predation levels.

The composition (e.g. ecological indicators such as conchostracans and amphibians) and the overall, low generic and specific diversity of the fauna is in good agreement with a supposed freshwater or brackish restricted depositional environment (Gall 1983; Briggs and Gall 1990; Anderson 1997). However, it is worth noting here that faunal assemblages differ from one concretion-bearing layer to another, a point that is discussed further below.

MATERIAL, PRESERVATION AND METHODS

Xiphosuran material

Since the first description of the material based on 13 specimens (Anderson 1997), extensive preparation work on the concretion collections by D. Sotty (Autun Museum) has made a large number of additional specimens available. Of the 23,250 sideritic concretions (15–45 mm in diameter) split to date that have yielded animal remains (Sotty *in* Chabard and Poplin 1999), 142 contain xiphosurans (0·61 per cent). All 142 specimens have been examined, with 60 of them carefully prepared for the purpose of this study. However, xiphosurans remain a rare component of the biota, which is largely dominated by crustaceans. Until now, only the Solnhofen Limestone of Germany (Jurassic), with more than 1000 specimens of *Mesolimulus walchi* (G. Viohl, pers. comm. 1999) recovered to date, and the Mazon Creek Konservat-Lagerstätte of north-eastern Illinois (Westphalian D equivalent) with 107 specimens belonging to five species (Baird and Anderson 1997), were the only localities with xiphosuran specimens in numbers comparable to those of the Montceau-les-Mines Lagerstätte. All of the material is in the D. Sotty collection, and belongs to the Muséum National d'Histoire Naturelle of Paris (MNHN-SOT); it is deposited in the Muséum d'Histoire Naturelle, 14 rue Saint-Antoine, F-71400 Autun (Chabard and Poplin 1999).

Preservation and taphonomy

With the exception of three specimens preserved in siltstones, the xiphosurans along with the majority of the fauna, are preserved within concretions. The three-dimensional (3D) aspect of their dorsal and ventral morphology and anatomy is unusually well preserved. The concretions are composed of siderite and pyrite with a few calcite veins and some phosphatic traces (El Hamet 1981; Couvrat-Desvergnes 1981); they are thought to have developed in deltaic environments where streams flowed into lakes (Gall 1983; Courel *et al*. 1985, 1994). About 36 per cent of the 142 available specimens are complete (outstretched or variably enrolled), with the tail piece still in connection and appendages preserved *in situ*. The experience gained during preparation shows that most specimens do have their appendages preserved (typically folded up within the prosomal cavity below the prosoma). This type of preservation suggests that: (1) post-mortem transportation was minimal; (2) post-mortem early mineralization probably facilitated the 3D preservation of anatomical features; (3) concretions started to build up before, or during, the earliest stage of the diagenetic processes.

Enrolled specimens are rare at Montceau (five of the 142 available specimens) whereas it is a common posture in numerous other Carboniferous xiphosurans such as *Euproops danae* (Bergström 1973; Sekiguchi *et al*. 1982). Moreover, the ecdysial suture is closed in all available specimens; this shows that they are individuals and not moulted exoskeletons. This original characteristic suggests that the xiphosurans from Montceau were trapped and buried alive by sudden mud flows (deltaic settings?) before they could fold up. In this way the preservation is noticeably distinct from that described for *Paleolimulus* from the Pennsylvanian–Permian Lagerstätten of Kansas (Babcock *et al*. 2000). In addition, this burial mode, as in many other Lagerstätten, would have created the conditions for their exceptional preservation.

Preparation

After the concretions were split, exposed specimens were prepared mechanically using dental tools, a compressed-air engraver pen, and fine needles in order to remove sediment and mineral deposits from both external and internal moulds. The mechanical preparation was often facilitated by specific chemical treatment. Thus, numerous specimens were cleaned by soaking split concretions in dilute hydrochloric acid, or formic acid, in order to dissolve out calcitic and carbonate infillings, or in the soap-like 'Quaternary O' to loosen phyllosilicate minerals. Internal moulds and latex replicas of both internal and external moulds were made and examined, and photographed conventionally and under the scanning electron microscope (Hitachi S800 SEM). Preserved juvenile specimens of the Recent limulid *Limulus polyphemus* (Linné, 1758) were obtained from the Carolina Biological Supply Company (USA) and used for morphofunctional comparisons with the fossil forms.

Terminology

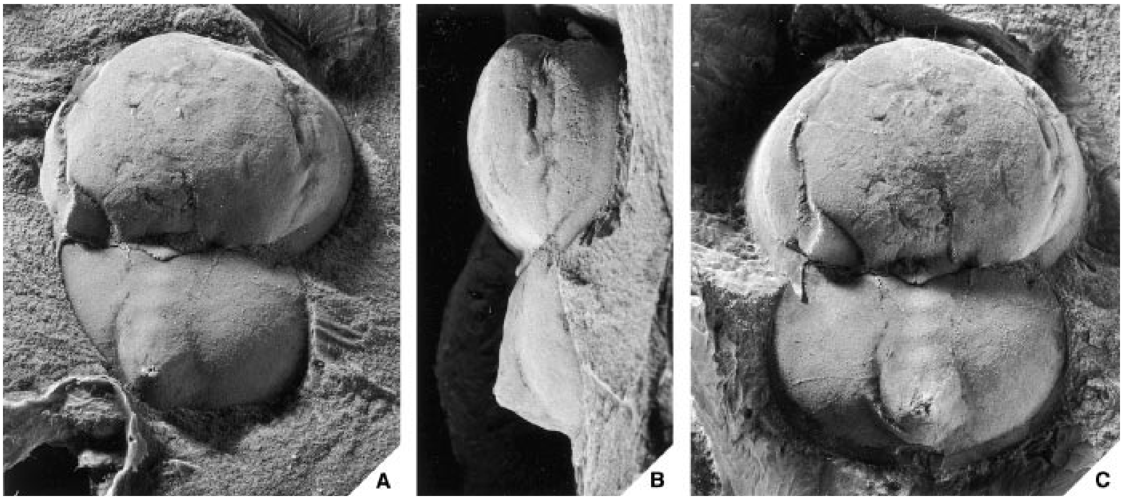
The morphological terms used for the description of *Alanops magnificus* gen. et sp. nov. follow those of recent studies (e.g. Anderson 1996, 1997; Anderson and Selden 1997) or monographs (Bergström 1975) describing fossil xiphosurans, and are consistent with the current terminology of extant xiphosurans (see Shuster 1982).

SYSTEMATIC PALAEONTOLOGY

Phylum CHELICERATA Heymons, 1901
Order XIPHOSURIDA Latreille, 1802
Suborder BELLINURINA Zittel and Eastman, 1913
Family EUPROOPIDAE Eller, 1938

Genus ALANOPS gen. nov.

Derivation of name. From the first name Alan (Latin, *Alanus*), and the suffix *-ops* (Greek, masc.), to honour Alan Racheboeuf.



TEXT-FIG. 2. *Pringlia birtwelli* (Woodward, 1872) (=*Liomesaspis birtwelli sensu* Anderson, 1997) from the Carboniferous Coal Measures of Coseley, Staffordshire, England; The Natural History Museum, J13882. A, latex replica from the external mould. B–C, internal mould, lateral and dorsal views. All ×3.

Type species. Alanops magnificus gen. et sp. nov., from the Stephanian B–C of Montceau-les-Mines, Saône-et-Loire, France (by monotypy).

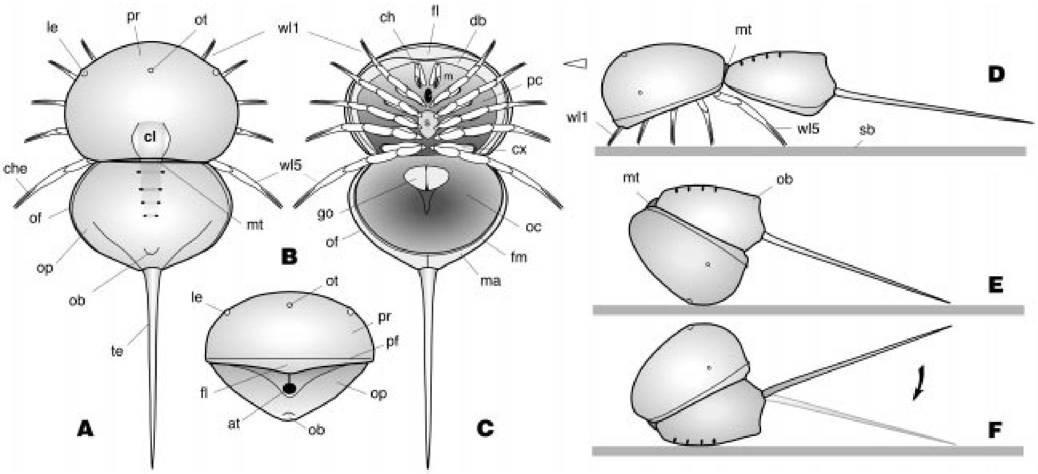
Diagnosis. Euproopid with subhemispherical prosoma and subtriangular, strongly vaulted opisthosoma, both lacking spines and ridges. No ophthalmic ridges. Vestigial genal spines present in early juveniles. Cardiac lobe poorly differentiated, posterolaterally bounded by short and shallow furrows. Opisthosomal axis posteriorly elevated, and poorly differentiated with four obscure axial rings, and four pairs of pit-like entapophyses. Long, styliform telson.

Discussion. *Alanops* gen. nov. resembles *Liomesaspis* Raymond, 1944 (e.g. a lateral opisthosomal flange with no lateral spines) but definitely lacks several key, diagnostic features of this genus such as the presence of ophthalmic ridges, ophthalmic spines and genal spines in adult specimens (see, for example, the reconstruction of the type species, *Liomesaspis laevis*; Anderson 1997, p. 433, fig. 7). New detailed observations of the material from Montceau-les-Mines led us to reconsider its previous generic assignment (Anderson, 1997). *Alanops* resembles *Pringlia* Raymond, 1944, in having a comparable outline, vaulted prosomal and opisthosomal shields, and a prominent termination of the opisthosomal axis. However, it lacks the typical genal spines and ophthalmic ridges of *P. birtwelli* (Woodward, 1872), the type species of *Pringlia* (compare Pl. 1 and Text-fig. 2). *Pringlia* was considered to be a junior synonym of *Liomesaspis* by Anderson (1997) and Anderson and Selden (1997); and Anderson (1997) proposed a new diagnosis for *Liomesaspis* (emended from Raymond 1944) based on the revision of the type species, *Liomesaspis laevis* Raymond, 1944, from the Westphalian D equivalent, Francis Creek Shale of Mazon Creek, Illinois, USA. *Alanops* gen. nov. possesses a set of original features that define it as a new euproopid genus.

Alanops magnificus sp. nov.

Plate 1, figures 1–8; Plate 2, figures 1–9; Plate 3, figures 1–13; Text-figures 3–4

1981 *Pringlia* sp.; Pacaud *et al*., p. 39.
1982 *Pringlia* sp.; Rolfe *et al*., p. 427.
v.1994 *Pringlia*; Poplin and Heyler, p. 145.
v.1997 *Liomesaspis laevis* Raymond, 1944; Anderson, figs 2–3.



TEXT-FIG. 3. Reconstruction of *Alanops magnificus* gen. et sp. nov. A, C, dorsal and ventral views. B, frontal view of specimen in inferred enrolled position. D, animal in life attitude, crawling on substrate. E–F, animal represented in enrolled position lying on substratum, resting on prosoma and opisthosoma, respectively. at, attachment of telson; ch, chelicerae; che, chelae; cl, cardiac lobe; cx, coxa; db, doublure; fl, frontal lappet of the subfrontal area; fm, opisthosomal free margin; go, genital operculum; le, lateral eye; m, mouth opening; ma, marginal area; mt, microtergite; ob, opisthosomal boss; of, opisthosomal flange; op, opisthosomal shield; ot, ocellar tubercle; pc, prosomal cavity; pf, prosomal flange; pr, prosomal shield; s, sternal plate; sb, substrate; te, telson spine; wl1-wl5, walking legs 1–5.

Derivation of name. Latin *magnificus*, magnificent, alluding to both the beautiful shape and exceptional preservation of these fossils.

Holotype. MNHN SOT 13446 (collections of the Musée d'Histoire Naturelle d'Autun, France); natural mould of a complete exoskeleton (Pl. 1, figs 2–3), and corresponding incomplete external mould (Pl. 1, fig. 4).

Locality and horizon. Saint-Louis opencast pit, north of Montceau-les-Mines (Saône-et-Loire, France), Assise de Montceau, bed 0 of Stephanian B–C age (Babin 1994; Doubinger 1994; Langiaux 1994).

Material. 142 specimens, all within sideritic concretions. Most specimens are from bed 0 of the Saint-Louis opencast pit. Three additional specimens (MNHN SOT 1785, 2160, and 4853) are preserved in siltstones.

Diagnosis. As for the genus.

Description

The description is based mainly on 38 complete, well-preserved specimens, 13 isolated prosomas, and nine isolated opisthosomas from the Saint-Louis pit, levels 0 and +2 (see Text-fig. 1). The largest complete carapace (MHNN SOT 1784; Pl. 2, figs 1–2) is 21·3 mm long (prosoma, opisthosoma and telson being 6·3, 5·8, and 9·2 mm long, respectively), and 9·0 mm wide (prosoma).

Prosoma. Globose shield with a subcircular outline. Length of available prosomas ranges between 2·3 and 7·5 mm, the maximum width being 10·8 mm. The prosoma MHNN SOT 78510 is 6·8 mm long and 9·4 mm wide (length/width ratio, 0·72), with the maximum width situated at about two-thirds of the length from anterior margin; the posterior margin is almost straight and 7·4 mm wide. Longitudinal profile strongly arched (width/height ratio about 2·75); the curvature increases gradually towards the frontal area. The posterior margin of the prosomal shield bends abruptly ventrally, forming a flat, vertical, and subtriangular wall partly closing the prosoma backwards.

Faint peripheral flange expressed as an almost straight, low and narrow ridge running all around the prosoma, and delineating the dorsal and subfrontal areas of the prosoma (Pl. 3, figs 1–2). In lateral view, the subfrontal area ventrally continues the curvature of the frontal area of the prosoma (Pl. 3, fig. 2). In anterior view, the subfrontal area projects ventrally forming a weak median beak and frontal lappet (Pl. 2, figs 1, 4; Pl. 3, fig. 2). Posterolateral angles of the prosoma are typically rounded, devoid of genal spines in larger specimens (Pl. 1, figs 1–3, 7, 9). However, the posterolateral angles of the smallest available prosoma (2·3 mm long and 3·5 mm wide; MNHN SOT 2163; Pl. 1, fig. 5) are weakly, but distinctly pointed. Cardiac lobe poorly differentiated, very weakly convex, smooth, devoid of any spine, and laterally bounded by short and faint furrows. Lateral furrows are best developed in their posterior half where they are almost straight, and converge markedly backwards. The width of the cardiac lobe never exceeds 1·8 mm along posterior margin of the prosoma. The cardiac lobe of specimen MNHN SOT 4860 is flanked with four pairs of very discrete, scar-like oblique furrows which could possibly correspond to apodemes (muscle attachment spots). These straight furrows converge backwards at an angle of about 45 degrees to the longitudinal axis of the prosoma.

Ophthalmic ridges and ophthalmic spines absent. Eyes are very small and lie in an outer, anterolateral position. In specimen MNHN SOT 77994 (length and width of prosoma 6·1 and 9·0 mm, respectively) the distance between eyes is 6·0 mm, and they are located 4·2 mm from the posterior margin of the prosoma. A median ocellar tubercle (Pl. 1, figs 5, 7; Pl. 2, fig. 4) is preserved in most specimens, and lies directly between the lateral eyes.

The free margin of the prosoma is very sharp and bordered by a narrow rim. Ventrally, the shield forms an internal doublure which grades into the softer, often wrinkled integument that covers the internal surface of the prosoma (MNHN SOT 1784: Pl. 2, figs 1–2, and 2154: Pl. 2, figs 6–8). The doublure is bounded inwards by a distinct, concentric groove, which is a possible convergent feature with the vincular furrow of post-Cambrian trilobites. Posterolateral parts of the integument exhibit oblique, striated features, which may indicate that the inner integument was flexible (Pl. 2, figs 1–2, 6, 8).

Opisthosoma. Vaulted shield, subtriangular to subsemicircular in outline, about 10 per cent smaller than the prosoma. Size differences are exemplified by several complete specimens such as MNHN SOT 4855 in which the opisthosoma is 5·1 mm long and 6·9 mm wide, whereas the prosoma is 6·0 mm long and 8·4 mm wide. Transverse profile highly convex, rounded-subtriangular. Opisthosomal axis poorly differentiated, weakly vaulted, and without lateral furrows. Lateral margins identified by the paired apodemes only. Four pit-like apodemes are discernible on either side of the axis (Pl. 1, figs 2, 4). Axial segments are hardly distinguishable in most specimens except MNHN SOT 2166 (Pl. 2, fig. 3), and MNHN SOT 13446 (Pl. 1, fig. 4), which both clearly show four segments in front of the fused unit overlying the telson base. The axis is narrow with a maximum width of about 1·2 mm for a corresponding opisthosomal width of 7 mm. The opisthosomal shield terminates abruptly as a small vertical area where the telson is inserted (Pl. 1, fig. 3). The last axial segment is prominent, and bears a spiny boss that, although short, projects backwards and slightly upwards. Lateral opisthosomal fields convex, smooth, devoid of any segmentation marks, limited outwards by a deep, rounded, peripheral furrow which separates them from the narrow, but well-differentiated flange. The peripheral flange is about 0·2 mm wide, smooth, without any spine or spine-insertion traces. A wide doublure is present and internally bounded by a distinct narrow concentric rim in a manner similar to that of the prosomal shield. Posteriorly, the marginal area of the opisthosoma becomes flat and forms a subtriangular, almost vertical, platform between the insertion area of the telson and the free ventral margin. This platform is split by a narrow medial furrow (Pl. 2, fig. 9).

The inner side of the opisthosoma of specimen MNHN SOT 2154 exhibits a pair of symmetrical subtriangular plates juxtaposed along their inner margins and overhanging an elongated feature (Pl. 2, figs 6–8). This pair of triangular plates closely resembles the genital operculum of Recent limulids (e.g. *Limulus polyphemus*; Text-fig. 6B) which, although fused, is a paired structure with two genital pores on the underside. The existence of two distinct operculate plates, instead of two fused plates as in the Recent *Limulus polyphemus*, could possibly be indicative of the plesiomorphic state of this character. The elongated feature may be similar to the genital ducts of Recent limulids. Owing to the lack of preserved remains of the book gills, this feature appears to lie flat on the inner side of the exoskeleton, but this may be a preservational artefact; it was possibly a ventral outer feature. In this way, the elongated feature bears some similarity to the sexually dimorphic stylet-like organ attached to the operculum of Palaeozoic eurypterids (see Braddy and Dunlop 1997) and similarly orientated posteriorly.

No remains of other internal organs or appendages (e.g. flap-like membranous appendages modified as gills as in typical xiphosurans) were found attached to the inner side of the opisthosoma.

Articulation of prosoma and opisthosoma. The dorsal side of complete, outstretched or enrolled exoskeletons shows no more than the median dorsal side of the microtergite (Pl. 2, fig. 3; Pl. 3, fig. 5). However, a complete external mould of the exoskeleton, including the mould of the microtergite (MNHN SOT 1881; Pl. 3, fig. 6) demonstrates that the microtergite is a small, transverse, both longitudinally and transversally arched, articulated element that links prosoma and opisthosoma. It seems to be functionally similar to the anterior half-ring of trilobite thoracic axial rings. The microtergite articulates below the posterior part of the cardiac lobe.

Telson. The telson is relatively large in relation to the carapace; it is styliform, smooth, and has a straight longitudinal axis. In lateral view, the distal part of the telson may gently bend dorsally. In specimen MNHN SOT 98594 (total length of the complete animal 11·2 mm) the telson is 10 mm long and 0·6 mm wide near its base. The telson has a flattened, even weakly depressed dorsal side near its base that is occupied by a tiny longitudinal ridge. Spine dorsoventrally flattened, elliptical in cross section with angular, acute, lateral margins. Dorsal process is a semicircular, subvertical, weakly elevated ridge (Pl. 1, fig. 6).

Appendages. Prosomal appendages are typically found clustered within the prosomal cavity and, strikingly, folded inwards in a similar way to those of preserved Recent limulids (compare Text-fig. 7B with Pl. 2, fig. 2). This configuration may be that of the animal just after death. The appendages are radially attached to the body and in a symmetrical manner along a curved line running from near the sagital plane of the animal (pair I = chelicerae) to near the posterolateral corners of the prosoma (pair VI = walking legs). Some of the appendages are complete and show no major post-mortem dislocation (e.g. walking legs; Pl. 2, fig. 5); others are broken and lack their distal part (Pl. 2, figs 1–2). In specimen MNHN SOT 1784 (Pl. 2, figs 1–2) a left walking leg is preserved in outstretched position and extends past the prosomal margin by about 5 mm (length of the prosoma 6·3 mm). It is clear from this specimen that the legs of *Alanops* were longer than those of other known extinct (e.g. *Weinbergina*; Stürmer and Bergström 1981) and extant (e.g. *Limulus*; Text-fig. 7B) xiphosurans. Chelicerae are preserved in several specimens, among which MNHN SOT 1784 (Pl. 2, fig. 2; Pl. 3, figs 3–4, 7) is the best example. However, owing to their very small size, they could not be fully prepared, and only their proximal parts appear on external moulds as well as on latex casts. They attach to the body anterior to the mouth (Pl. 3, fig. 7) and form a pair of short appendages lying almost parallel to each other and to the sagittal plane of the animal. The chelicerae are followed by five uniform pairs of long walking legs (numbered II–VI), each composed of articulated segments (terminology follows Stürmer and Bergström 1981). The specimen MNHN SOT 5168 exhibits a complete left set of five walking legs preserved *in situ* (Pl. 2, fig. 5), and two legs belonging to the right set. The last segment of each appendage (= tarsus) is between 3·0 and 4·0 mm long, and is terminated by long chelae (about 1·5 mm). One of the walking legs of specimen MNHN SOT 2161 (possibly pair III) is complete; the length of each segment is 1·5 mm (coxa), 1·25 mm (trochanter), 1·4 mm (femur), 1·9 mm (patella) and about 3 mm for the tarsus, the chelae being about 1·25 mm long; hence the total length of the leg in outstretched position was possibly 10·3 mm. In specimen MNHN SOT 1784 (Pl. 2, figs 1–2) the two last segments of the walking leg (probably belonging to pair VI) are respectively 2·05 mm (tibia) and 3·75 mm (tarsus) long for corresponding diameters of 0·45 mm and 0·5 mm respectively; chelae are 1·5 mm long with a maximum diameter of about 0·12 mm. Segments are subcylindrical or often flattened as, for example, the tarsus of specimens MNHN SOT 4054 and 4055 (Pl. 3, figs 11 and 13, respectively), probably owing to the post-mortem collapse of internal tissue, or to slight compression.

The inner margins of the coxae of the prosomal appendages II–IV are blade-like (Pl. 3, fig. 4) and may correspond to gnathobases. They point radially to a medial groove occupied (posterior to the base of the third pair of appendages) by a prominent sternal plate, possibly similar to the promeso-sternite of Recent limulids (see Shuster 1982).

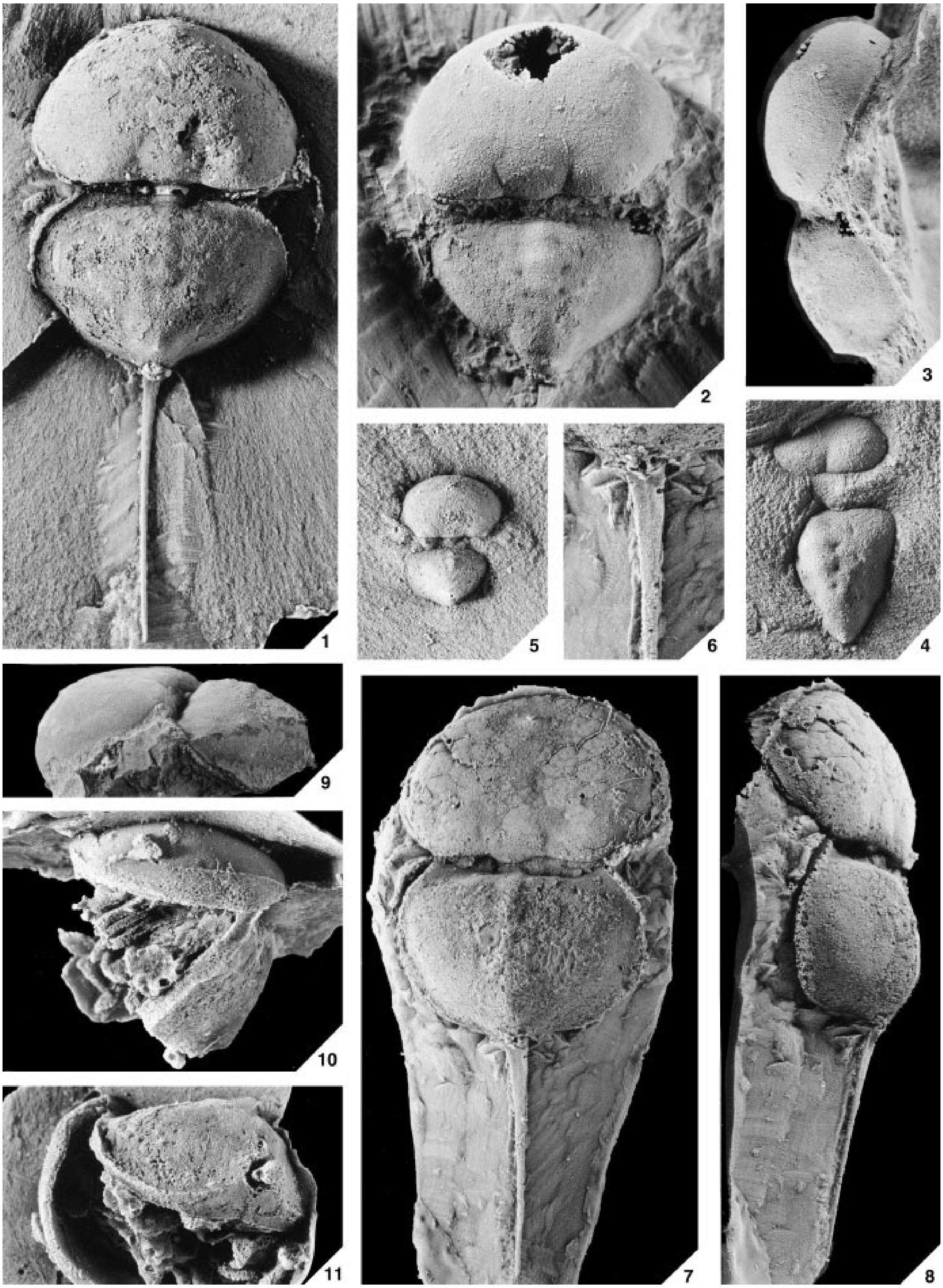
Size distribution and ontogenetic changes

Sixty uncompressed specimens preserved in concretions were considered suitable for biometric analysis. Measurements of 38 complete exoskeletons, 13 isolated prosomas and nine isolated opisthosomas were made using simple

EXPLANATION OF PLATE 1

Figs 1–11. *Alanops magnificus* gen. et sp. nov., Stephanian B–C, Assise de Montceau, Montceau-les-Mines, France. 1, MNHN SOT 88526, a complete, fully outstretched carapace. 2–4, MNHN SOT 13446, holotype, dorsal and lateral views of the natural mould of a complete carapace, and incomplete external mould. 5, MNHN SOT 2163, juvenile specimen with pointed posterolateral angles of the prosoma, original of Anderson, 1997, fig. 3D. 6–8, MNHN SOT 1951, proximal part of the telson, and dorsal and lateral views of the complete exoskeleton. 9, MNHN SOT 12882, lateral view of the natural mould of a complete exoskeleton. 10–11, MNHN SOT 80817, lateral and posterior views of a partly enrolled specimen. All are light photographs of latex replicas except 2–3, and all ×5 except 6, which is ×8.

PLATE 1



RACHEBOEUF *et al.*, *Alanops*

parameters such as the prosomal and opisthosomal length and width, and the length of the tail spine. Although the sample is composite and does not reflect a true population, and the number of specimens is not always significant, the biometric data below are given for first time for a Palaeozoic xiphosuran.

There are no discernible morphological differences between large and small specimens except that in two very small prosomal shields (less than 3 mm long), the cardinal angles are markedly pointed and not rounded as in larger individuals (compare Pl. 1, figs 2 and 5).

The prosomal and opisthosomal lengths range from 2·3 to 7·5 mm, and from 2·1 to 6·0 mm respectively, suggesting that several ontogenetic stages are present in our sample. The frequency of prosomal and opisthosomal length (Text-fig. 4A) and width (Text-fig. 4B) does not show a normal distribution. The Kolmogorov-Smirnov One Sample Test using normal (0·00, 1·00) distribution was applied to our sample. Lilliefors probability values are 0·000, 0·000, and 0·002 for the distribution of prosomal length and width, and opisthosomal length respectively. Only the distribution of the opisthosomal width, with a probability of 0·063 could be considered as normally distributed. These results probably reflect both the sampling and taphonomic conditions.

Scattergrams for length vs. width ratios for prosomas (Text-fig. 5A) and opisthosomas (Text-fig. 5C) display rectilinear and almost parallel curves, indicating a similar growth pattern for both shields. There is a good correlation between these two parameters (0·91 and 0·87 for the prosomas and opisthosomas respectively). Although the sample is not significant (nine measurements), the correlation is even better (0·97) when the prosomal width is compared to the developed longitudinal length of the prosoma (Text-fig. 5B). However, the plots do not fall within a series of individual clusters as is often the case for natural populations of arthropods (e.g. ostracods; Martinsson 1962; Smith and Martens in press) that grow in size through successive moults. The majority of our specimens concentrate within a relatively narrow size range (for example 72 per cent of the prosomal lengths fall between 5 and 7·5 mm) and both very small (0·06 per cent < 3·5 mm) and large individuals (15 per cent > 6 mm) are rare. This may also be an artefact related to the composite nature of the sample and to sample size.

As for the telson, the correlation coefficient has the same value when the spine length is compared to the total carapace length ($R^2 = 0{\cdot}708$; Text-fig. 5D), or to the prosomal length ($R^2 = 0{\cdot}702$). The scattergram of Text-figure 5E, clearly shows that the prosomal outline expressed by its length vs. width ratio changes during growth. In the smallest specimens (length < 5 mm), the length vs. width ratio ranges between 0·630 and 0·667 (mean 0·65 for seven specimens). For moderate-sized specimens (5 mm < prosomal length < 6 mm) the ratio ranges from 0·654 to 0·755 (mean 0·674 for 23 prosomas), and for the largest specimens (prosomal length > 6 mm), the ratio ranges from 0·678 to 0·775 (mean 0·727 for 19 prosomas). Such a variation means that from a prosomal length of about 5 mm, the prosomal width grew more rapidly than its length; this points to a positive allometry and is in good agreement with biometric studies on Recent limulids (Sekiguchi *et al*. 1982; Shuster 1982).

The multivariate analysis using prosomas and opisthosomas of complete exoskeletons allows discrimination of five groups of individuals which are well expressed on the PCA diagram (Text-fig. 6), with a probability of 95 per cent, and may correspond to successive growth stages that were undetected on bivariate scattergrams. However, more specimens are needed to identify ontogenetic stages with accuracy.

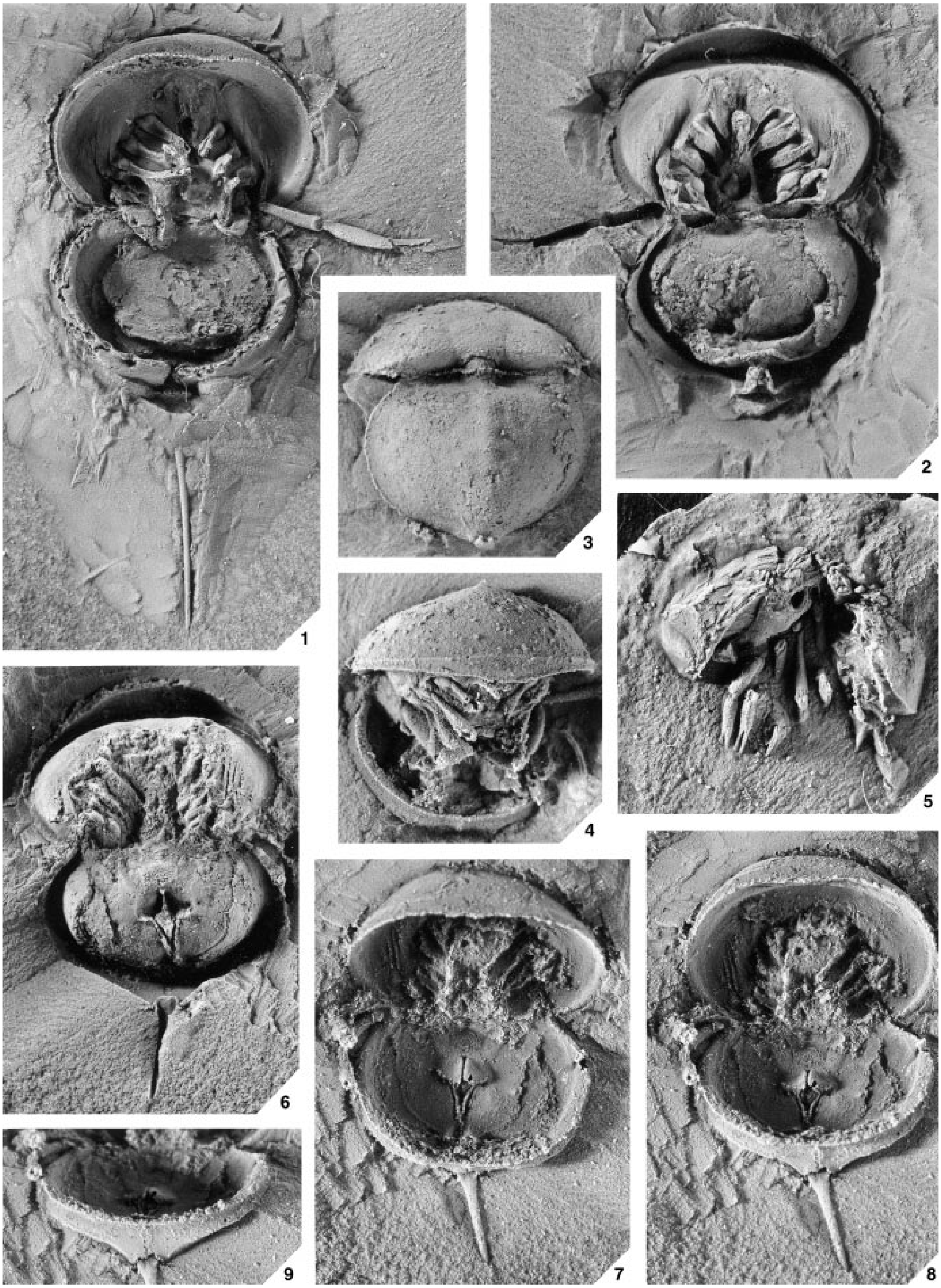
Although very few studies using biometrics have been made concerning the ontogeny of Recent limulids (Sekiguchi *et al*. 1982; Shuster 1982), the measurements of the incremental growth of a female (*Limulus polyphemus*) raised in an aquarium for eight years indicate that the animal grows through at least 16 post-embryonic stages with a positive allometric growth of the prosoma (Shuster 1982, fig. 19) comparable to that of *Alanops*. Adult males may not moult after reaching maturity. Data obtained on the growth stages within a large population of limulids, when plotted on diagrams, show a size distribution (prosoma) in distinct clusters for several growth stages.

Populations dominated by adults are frequent in Recent limulids. For example, sexually mature males and females are known to migrate to shallow water and to congregate along the shores of sounds, bays and even estuaries (spawning sites). A similar sexual and migratory behaviour may explain why *Alanops* is mainly represented by adults in the

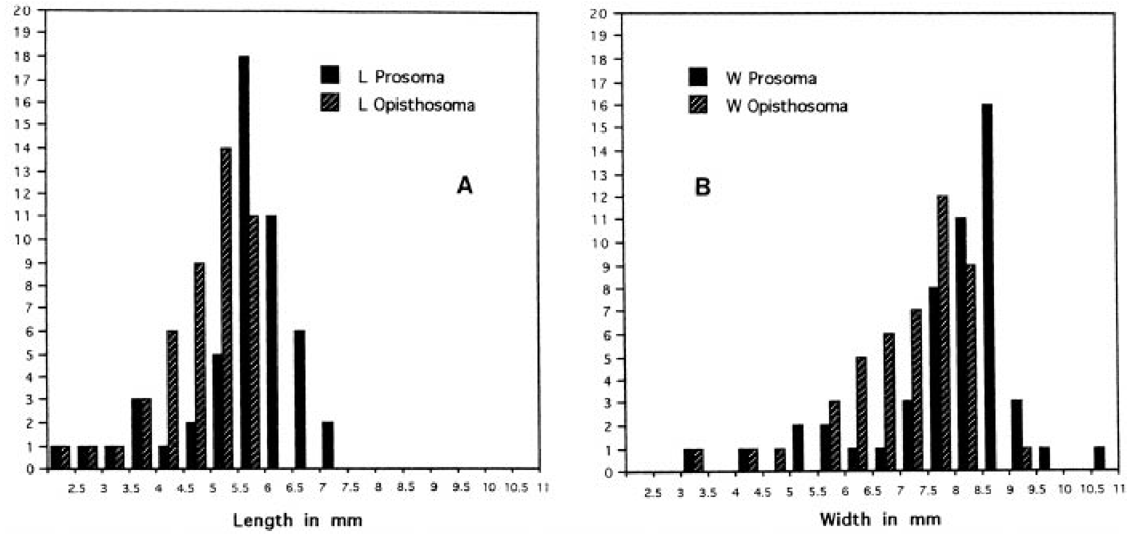
EXPLANATION OF PLATE 2

Figs 1–9. *Alanops magnificus* gen. et sp. nov., Stephanian B–C, Assise de Montceau, Montceau-les-Mines, France. 1–2, MNHN SOT 1784, latex cast and external mould of the ventral side of a complete specimen. 3–4, MNHN SOT 2166, partly enrolled specimen in dorsal and anteroventral views (dorsal view exposes the posterior margin of the prosoma as well as the microtergite). 5, MNHN SOT 5168, a specimen broken longitudinally, with five walking legs protruding beyond the carapace margin. 6–9, MNHN SOT 2154 (= AM 5779, fig. 2B of Anderson 1997), ventral external mould of a weakly enrolled specimen. 6, internal mould in dorsal view; 7–8, the same in ventral view showing the genital operculum; 9, posterior margin of the opisthosoma in posteroventral view. All are light photographs of latex replicas except 2 and 6, and all ×5.

PLATE 2



RACHEBOEUF *et al.*, *Alanops*



TEXT-FIG. 4. *Alanops magnificus* gen. et sp. nov. Size distribution for 51 prosomas and 47 opisthosomas. A, according to their length (L). B, according to their width (W).

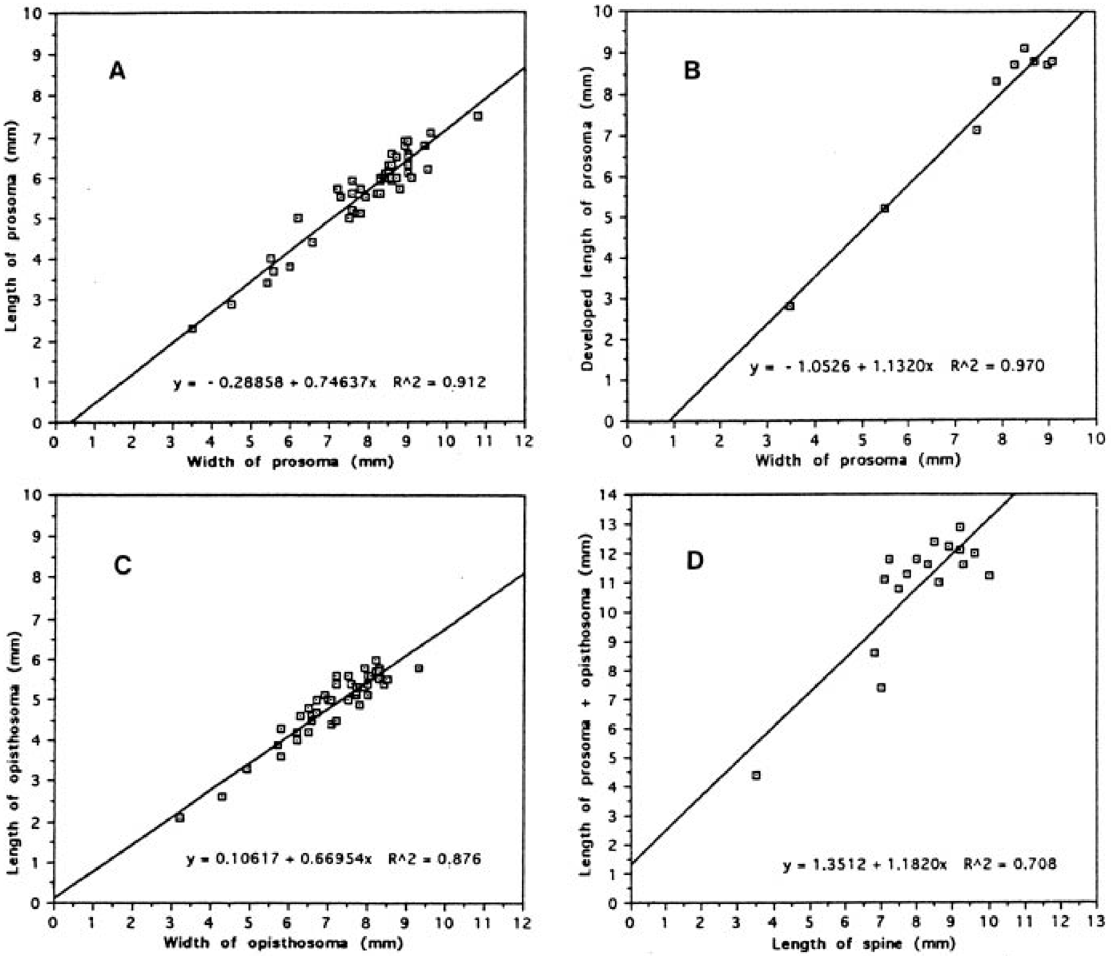
Montceau biota. The relative scarcity of juveniles in the preserved palaeoenvironment may result from preservational factors or reflect their scarcity in the original environment, or imply that they lived elsewhere; the influence of physical factors (e.g. preservation, selective sorting) appears more likely since we consider that the largest specimens had possibly been trapped and buried alive by sudden mud flows.

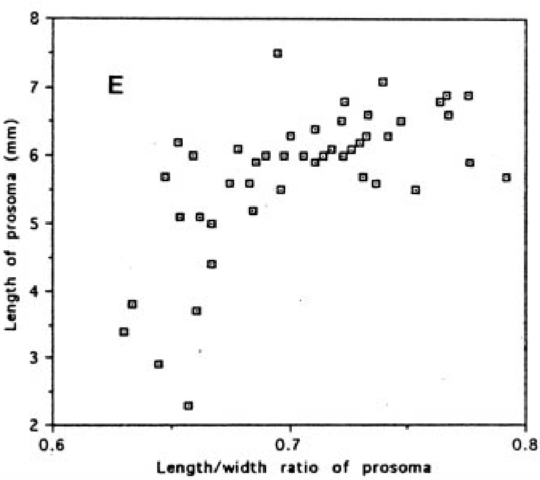
PHYLOGENY

The phylogeny of Palaeozoic Xiphosura was recently studied by Anderson and Selden (1997) based on 19 taxa including the species from Montceau-les-Mines, at that time assigned to the genus *Liomesaspis*. Anderson and Selden (1997, pp. 427–428, figs 3–4, table 1) used 26 characters to establish their cladogram, and the two outgroups *Lemoneites* and *Paleomerus* to polarise the characters. Character 5 is the secondary loss of lateral opisthosomal spines. *Euproops* has lateral spines, *Liomesaspis* has secondarily lost the lateral spines of the opisthosoma. *Alanops magnificus* shares this character (synapomorphy) with *Liomesaspis*, while four other apomorphic characters distinguish *Alanops* from both *Euproops* and *Liomesaspis*. These characters in *Alanops* are: 9, the absence of ophthalmic ridges; 12, the absence of ophthalmic spines; 13, the straight posterior margin of the carapace; and 14, the rounded genal angles of largest prosoma.

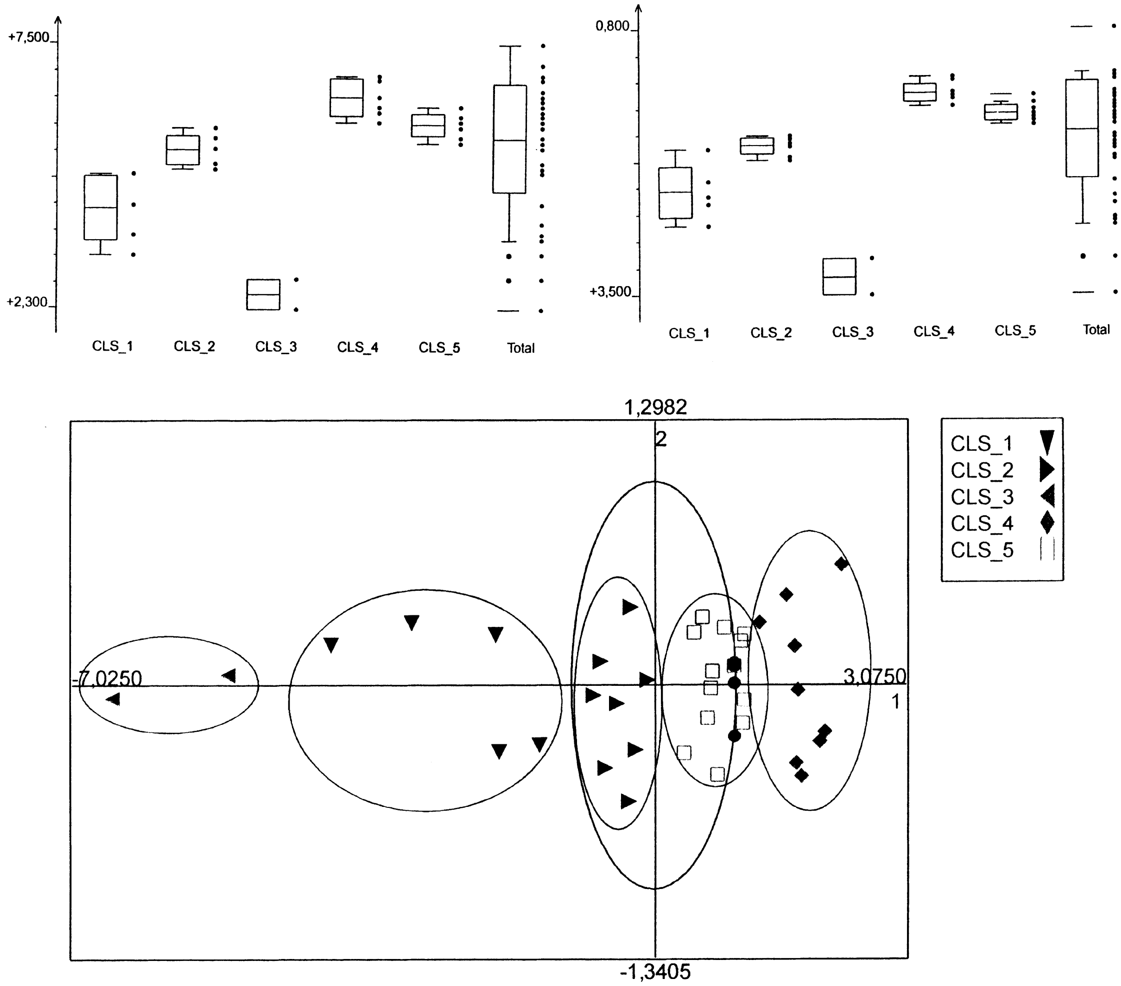
The lack of the precardiac lobe in *Alanops* corresponds to state 2 of character 19, and characterizes Xiphosurida. As defined by Anderson and Selden (1997, p. 26), the opisthosomal flange (character 23) is a synapomorphy of *Alanops*, *Euproops*, and *Liomesaspis*. The lack of opisthosomal axial carina (character 26) in *Alanops* corresponds to the plesiomorphic condition according to Anderson and Selden (1997).

Alanops exposes several apomorphic characters (9, 12, 13, 14) and retains a least plesiomorphic character (26–0; lack of opisthosomal axial carina), which make it different from both *Euproops* and *Liomesaspis*, although it undoubtedly belongs to the same group, along with *Bellinurus* (Anderson and Selden 1997, fig. 4). The genal angles are pointed in the smallest, juvenile specimens, and become completely rounded in the largest specimens. This polymorphic character is interpreted here as an autapomorphy for the genus. The genal spines and ophthalmic spines in xiphosurans usually grow throughout the life of the organism. The lack of genal spines in the largest specimens of *Alanops* has led us to consider that they are sub-adult or adult forms. Both the unusual small adult size and prosomal ontogeny





TEXT-FIG. 5. *Alanops magnificus* gen. et sp. nov. A–E, bivariate analysis. A, scattergram of lengths and widths for 51 prosomas. B, scattergram of developed lengths and widths for nine prosomas. C, scattergram of lengths and widths for 47 opisthosomas. D, scattergram of total lengths of the shield and lengths of tail spine for 17 complete specimens. E, scattergram for prosomal lengths and prosomal length/width ratios for 51 prosomas.

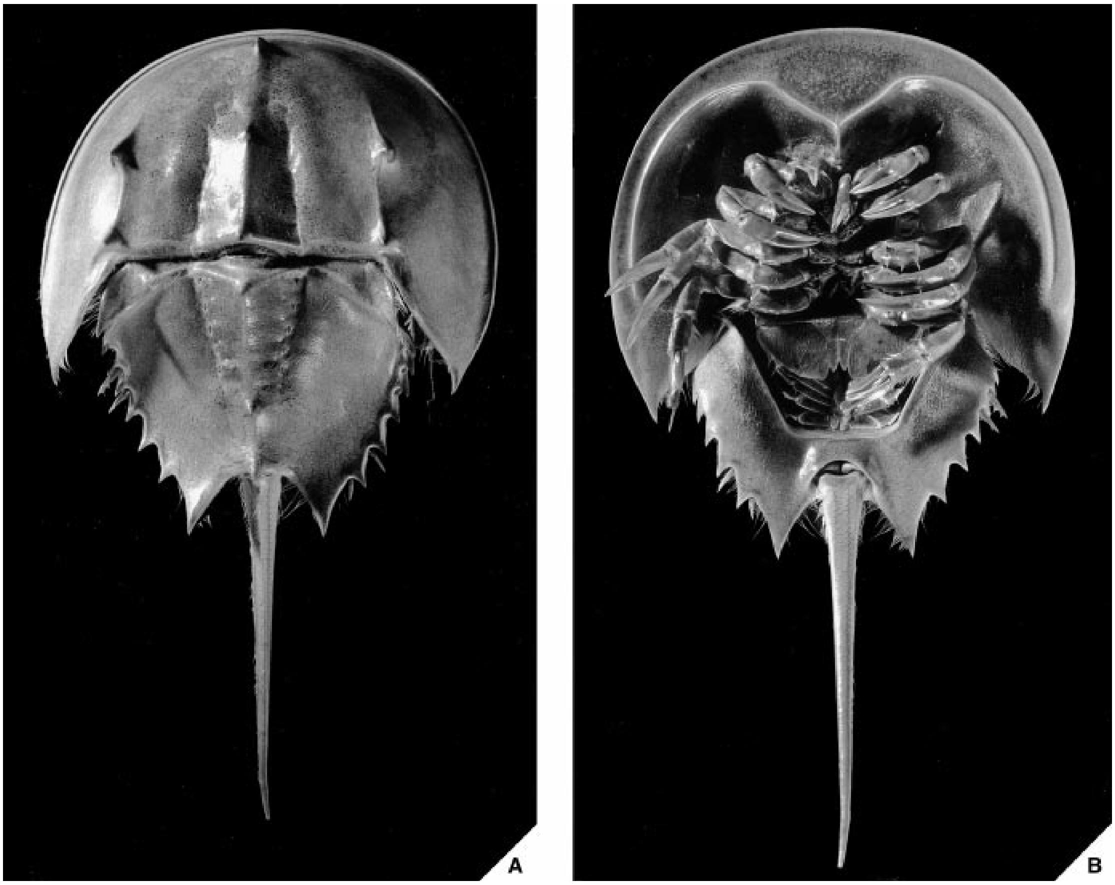


TEXT-FIG. 6. *Alanops magnificus* gen. et sp. nov. Multivariate analysis for 51 prosomas. Definition of five identified groups defined using a PCA diagram combining prosomal and opisthosomal data (length and width) for 38 complete specimens.

of *Alanops* point to a paedomorphic derivation from the bellinurine xiphosuran stock. *Alanops* is perhaps closest to being a sister taxon of *Liomesaspis*. However, further revision of Palaeozoic xiphosuran taxa is required before the exact phylogenetic position of *Alanops magnificus* can be determined.

BODY PLAN

Despite important differences in size and external ornament (spines, ridges), the body plan of *Alanops* is close to that of Recent limulids except for the loss of spines and the anatomy of the ventral operculum. Similarities are expressed in the exoskeleton, in details of the appendage structures, and in other parts of the internal anatomy. Important aspects of the body plan of modern xiphosurans can be traced back at least to the Carboniferous. Conservatism applies to the tagmosis, segmentation (chelicerae + five pairs of walking legs) and appendage configuration (short chelicerae and five-segmented walking legs with



TEXT-FIG. 7. *Limulus polyphemus* (Linnaeus) from Florida (USA), Recent. Juvenile specimen in dorsal (A) and ventral (B) views, natural size.

gnathobase). The major difference between *Alanops* and Recent limulids lies in the articulation system that connects the prosomal and opisthosomal shields, and in the ability to roll up in *Alanops*, but not in Recent limulids. *Alanops* also apparently lacks chilaria and specialized features such as a distal petal-like process and spatulate flabellum on the fifth pair of walking legs. However, the flabellum may not be a specialized feature but the vestigial remnant of an exopod ramus; in this way the flabellum would be a retained plesiomorphy.

In all Recent limulids, as exemplified here by a juvenile specimen of *Limulus polyphemus* (Text-fig. 7B), the subfrontal area (separated from the dorsal shield by the prosomal peripheral flange) is flat, or weakly concave, and lies in a horizontal plane on the ventral side of the prosoma. This is also probably the case in most Palaeozoic limulids. It is a feature that is strongly reminiscent of the frontal lappet and prosomal margin of *Alanops*, although their orientations differ: almost vertical and convex in *Alanops*; bent inwards and concave in *Limulus* (compare Pl. 2, figs 4, 7–8 and Pl. 3 figs 2–3 with Text-fig. 7B). To us, both features may be homologous. If it is indeed a homology, then it is reasonable to assume that the ventral position of the subfrontal area of modern limulids was produced by the rotational motion of *c*. 90 degrees of the prosomal anterior margin through evolution. When comparing the exoskeleton morphology and profile of Palaeozoic limulids, it is clear that most of them exhibit a flattened prosomal margin, suggesting that, in common with Recent limulids, they were initially burrowers. The rotation observed in *Alanops* and closely related forms such as *Pringlia*, may be closely related to changes in the lifestyle of xiphosurans, for example, from burrowing to crawling as supposed here for *Alanops*.

Among the fossil xiphosurans with a well-preserved ventral anatomy, it should be noted that *Weinbergina* from the Devonian of Germany (Stürmer and Bergström 1981) exhibits six pairs of walking legs devoid of chelae, instead of the five chelate pairs observed in *Paleolimulus*, *Alanops* and Recent limulids.

FUNCTIONAL MORPHOLOGY, LIFE STYLE AND ECOLOGICAL NICHE

Locomotion

Alanops supported its body on five pairs of prosomal legs (Text-fig. 3) that were clearly adapted for crawling (long podomeres, sigmoidal outline) and seizing prey or particles (long chelae) rather than for burrowing or swimming. Unfortunately it was not possible to obtain an approximation of the body mass of *Alanops*, but its carapace was very thin. An analogue can be found in some brachyuran crabs with a relatively heavy body mass and slender walking legs; they are active crawlers in both submerged and terrestrial environments. Most Palaeozoic xiphosurans alleged to have been capable of swimming (Fisher 1977) often exhibit long genal spines, well-developed ophthalmic spines, and marginal opisthosomal spines. These features are absent in *Alanops*. Crawling activities would have corresponded to the fully outstretched position of the exoskeleton (Text-fig. 3D). The hemispherical shape of the prosoma, added to the development and position of the subfrontal area with a median lappet, is poorly consistent with superficial burrowing activities typical of living limulids equipped with a penetrative headshield and prosomal arch (Vosatka 1970; Fisher 1975), as illustrated herein by *Limulus polyphemus* (Text-fig. 7). The fifth pair of legs, apparently longer than the remaining walking legs, are likely to have played a role in stabilizing the animal on the substrate and may have acted as a lever to facilitate enrolment and subsequent return to the upright position (see Text-fig. 3).

Feeding

The presence of chelicerae overhanging the mouth opening, opposing sets of blade-like gnathobases facing the sagittal food groove, and prehensile chelae all indicate a feeding apparatus comparable with that of modern limulids. The sternal plate was probably strongly sclerotized and may have played a significant role in the feeding mechanism. In Recent limulids, food is ground up by the converging movement of coxae, with the spines of the moving gnathobases directing food to the mouth. The chelate walking legs are used as clasping appendages to transfer small invertebrates from the sediment to the food groove. Recent limulids are generalist feeders (Botton 1984; Botton and Haskin 1984). The most important prey item found in the digestive tracts of Recent horseshoe crabs are bivalves (more than 80 per cent), followed by

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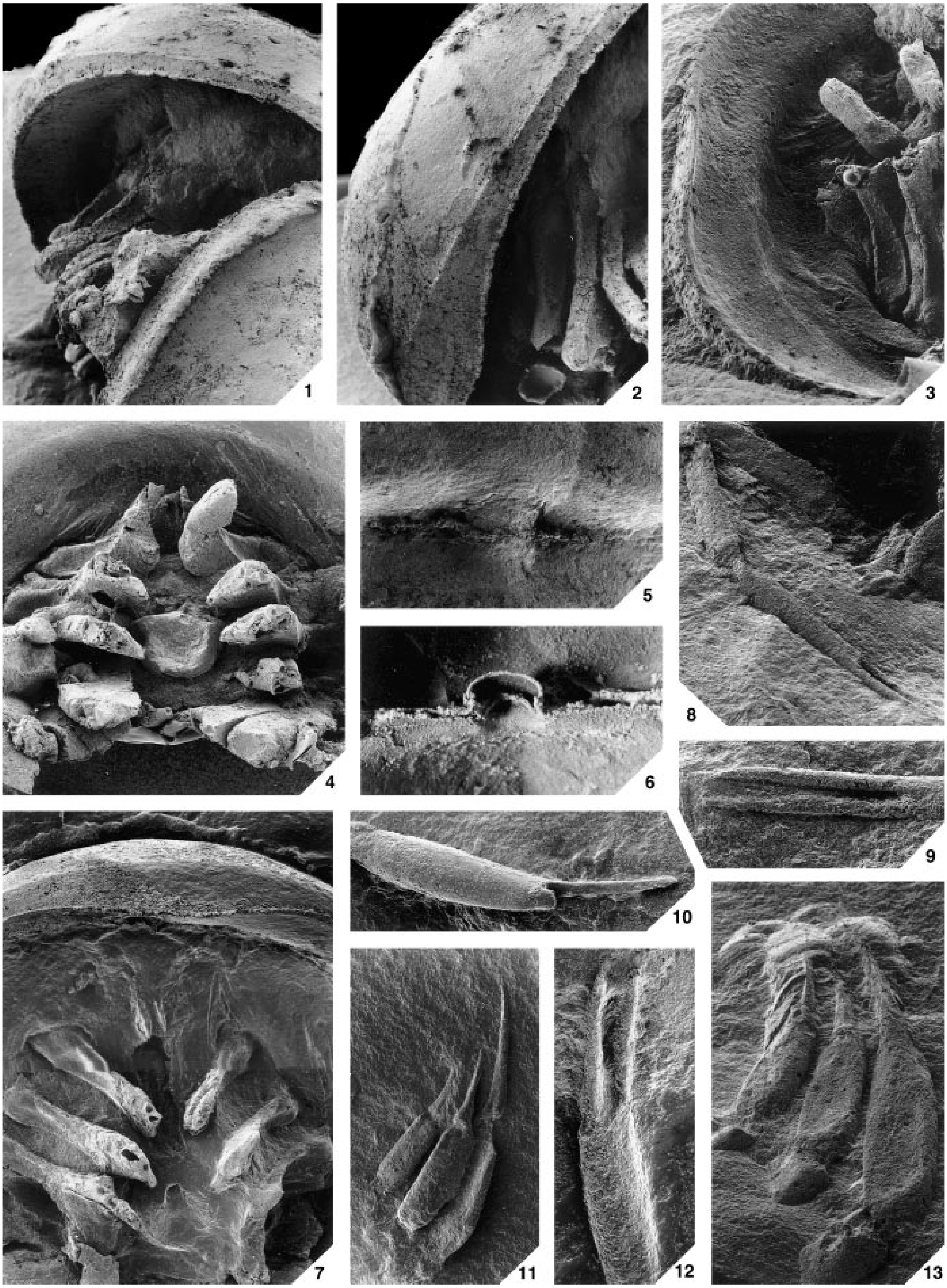
EXPLANATION OF PLATE 3

Figs 1–13. *Alanops magnificus* gen. et sp. nov., Stephanian B–C, Assise de Montceau, Montceau-les-Mines, France. 1–2, MNHN SOT 2166, lateroventral and anterolateral views of a partly enrolled complete exoskeleton showing prosomal and opisthosomal ventral margins, and the flange and the subfrontal area, respectively; ×20. 3–4, MNHN SOT 1784. 3, inner side of the prosoma showing the doublure and the first pairs of prosomal appendages; ×20. 4, prosomal appendages I–VI; ×20. 5, MNHN SOT 2166, partially enrolled specimen in dorsal view showing the articulation between prosoma and opisthosoma, the straight hinge line and the microtergite; ×22. 6, MNHN SOT 1881, dorsal external mould of a complete exoskeleton showing the external mould of the microtergite; ×10. 7, MNHN SOT 1784, inner side of the prosoma; ×13·5. 8–9, MNHN SOT 1656, an almost fully extended complete left walking leg (possibly fifth pair of prosomal appendages); ×22, and enlarged view of the chelate extremity; ×35. 10, MNHN SOT 1784, broken chelae of fifth left walking leg; ×25. 11, MNHN SOT 4055, right set of three walking legs; ×20. 12, MNHN SOT 5168, complete chelate extremity of a left second walking leg; ×40. 13, MNHN SOT 4054, left set of three walking legs; ×30. All scanning electron micrographs of latex replicas except 6.



RACHEBOEUF *et al.*, *Alanops*

gastropods, polychaetes, crustaceans and miscellaneous taxa (Botton and Ropes 1989). No fossil evidence is available on the diet of *Alanops*. Because of its relatively small size it may have fed on soft-bodied invertebrates such as worms, small crustaceans (e.g. ostracods, conchostracans; Vannier *et al*. in prep.), arthropod larvae that were represented in the Montceau biota, or on decaying material of various origins. Although bivalves abound in places at Montceau (Babin 1994), their size range (7·75–21·25 mm in length) excludes the possibility that they constituted a major food source for *Alanops*.

Vision

The visual organs of *Alanops* consist of small, widely separated lateral eyes and a median ocellar tubercle, and superficially resemble those of Recent limulids (compare Pl. 1, figs 2, 7 with Text-fig. 7A). If the eye structure was the same as in Recent limulids, with few ommatidia, the position of the lateral eyes on the prosomal shield is likely to have provided the animal with a wide field of vision. However, the lateral eyes of Recent limulids contain too few ommatidia for image formation and are used essentially to detect movement (Ruppert and Barnes 1994).

Enrollment and coaptation

Several complete specimens of *Alanops magnificus* are preserved partly enrolled with their appendages withdrawn into the prosomal cavity (e.g. MNHN SOT 2154 and 2166; Pl. 2, figs 3–9). The gape between the two shield margins varies from about 120 to 70 degrees (MNHN SOT 2166). Although no specimen was found completely closed, *Alanops* displays a set of adaptive features which suggest that complete enrollment of the exoskeleton was possible as in many other Palaeozoic xiphosurans.

1. The articulation between the prosoma and the opisthosoma consists of a single joint formed by a straight transverse hinge line and a stout central microtergite that together enabled the two shields to rotate relative to each other with a large angular amplitude of movement.
2. Coaptive devices indicate that the prosomal and opisthosomal margins were able to fit into each other. The size difference between the two shields (opisthosoma *c*. 10 per cent smaller than prosoma) is exactly sufficient for the marginal area of the prosoma to overlap that of the opisthosoma (prosomal frontal lappet fitting tightly onto the subtriangular opisthosomal platform, just below the tail spine). Lateral interlocking of the two shields may have been facilitated by the groove-like marginal area of the opisthosoma, thus possibly hindering lateral slippage in the enrolled posture. In addition, the peripheral flange of the opisthosoma is likely to have acted as a stop-feature. Internally, the doublure of the prosoma is flattened, fringed with a rim (Pl. 3, fig. 2), and therefore appears to have been well designed to accommodate the opisthosomal free margin.
3. The strong vault in both the prosoma and opisthosoma created a sufficiently large cavity in between to accommodate the appendages when the animal was completely enrolled.

Coaptive devices are well-documented in other Palaeozoic arthropods such as trilobites but have not been demonstrated previously in xiphosurans. The low-level articulation system of the two shields also allowed the almost complete outstretching of the animal; in this position, the whole set of appendages (prosomal legs and opisthosomal limbs) would be exposed and able to function (Pl. 2, figs 1–8; Text-fig. 3).

The ability to enrol may have been acquired as a response to environmental stress, both biotic (against predation) and abiotic (against desiccation during subaerial exposure). Spherical enrolment or folding-up is unknown in Recent limulids at any developmental stage but, although poorly documented, is known to have occurred in other Palaeozoic xiphosurans such as *Euproops danae* (Bergström 1973; Sekiguchi *et al*. 1982) and *Bellinurus* (Anderson and Selden 1997). Enrolment is interpreted mainly as a possible response to predation and may have allowed the animal to withstand unfavourable conditions such as temporary emersion (gills kept moist). Enrolment is used by numerous Recent terrestrial isopods to prevent desiccation.

ECOLOGY

Depositional environment

The environmental setting of the Montceau biota was that of an intramontane basin. Evidence comes from the presence of extensive fluvial and lacustrine, and locally plant-rich deposits within the Blanzy-Montceau Basin (Courel 1983; Courel *et al*. 1985, 1994). There is no indication in the geology of this basin of any marine influence that could be deduced from the lithological sequence, the structural background or the palaeogeography. In this context, the sideritic fossiliferous concretions of the Montceau Lagerstätte appear to have formed in a lacustrine/deltaic complex (streams flowing into lakes) (Gall 1983; Courel *et al*. 1985).

Faunal composition and faunal associates of Alanops

The presence of terrestrial animals (arthropleurids, insects, scorpions and other arachnids, and millipedes), amphibians and plant remains from inferred surrounding swamps and dense forests is a strong indicator of land in the vicinity. Although post-mortem transportation is often evident, the excellent preservation of the fossils indicates that the natural environment of the terrestrial animals was probably relatively close to where they were deposited. The fauna is dominated by aquatic organisms (e.g. crustaceans, molluscs, fishes). Some groups, such as the conchostracans, are considered reliable indicators of fresh water conditions since almost all Recent conchostracans live in fresh water (essentially temporary water-bodies). Syncarids (abundantly represented in the Montceau biota) have modern representatives that are found almost exclusively in fresh water. The infaunal bivalve *Anthraconaia* characterizes freshwater environments in Europe, although North American occurrences from Kentucky (USA) are apparently associated with 'brackish or salted' environments (Eagar 1973, p. 409).

Only a very small percentage of organisms belong to groups that normally characterize marine conditions. These are worms (questionably polychaete annelids) but they have not yet been studied. Euthycarcinoids form an extinct group whose ecological preferences rely on indirect evidence, but they were probably freshwater inhabitants, except in Mazon Creek (Rolfe *et al*. 1982, 1985). There is a definite Devonian freshwater example from hot spring deposits at Rhynie, north-east Scotland. Obviously these organisms raise the question of the existence of possible brackish conditions in the Montceau Basin, at least locally in space and time. However, no element of the biota has been found so far that indicates a possible marine incursion in the Montceau Basin (Heyler 1986; Heyler and Poplin 1988; Poplin 1994).

It is important to note here that the distribution of organisms through space and time is not homogenous at Montceau (Couvrat-Desvergnes 1981). As a rule, a clear distinction has to be made between quantitative data on the fauna as a whole, and the data obtained from each of the eleven fossiliferous concretion-bearing beds. Quantitative data compiled by Sotty (pers. comm. 1999; Table 1) allow comparison between the faunal composition of two concretion beds from the Saint-Louis opencast, namely beds 0 and +2. The Saint-Louis opencast pit yielded an especially abundant and diverse fauna. The numbers given in Table 1 refer to the relative number of identifiable animals or animal fragments found in beds 0 and +2, and at the Saint-Louis pit as a whole.

Most groups are present in bed 0 except onychophorans, arachnids and agnathans. The fauna recovered from bed +2 is much less abundant (Table 1). Although the absence or relative percentage of one particular taxon may be influenced by the size of sample, bed 0 seems to be characterized by the relative scarcity of conchostracans, euthycarcinoids and amphibians whereas these three groups are well represented in bed +2. Conversely, bivalves and xiphosurans are abundant in bed 0 but are missing (bivalves) or very rare (only one xiphosuran specimen) in bed +2. The faunal associates of *Alanops* (1 per cent of the total fauna) deduced from the faunal content of bed 0 are: syncarids (48·5 per cent), bivalves (43·3 per cent), annelids (3·6 per cent), insects (1·7 per cent), ostracods, isopods, myriapods, conchostracans, euthycarcinoids, fish and amphibians. The vertical distribution of organisms through bed 0 (*c*. 40 cm thick) is not documented except that prolific *in situ* assemblages of the bivalve *Anthraconaia* occur within the lowermost 5–10 cm (Couvrat-Desvergnes 1981; Babin 1994). Among the 1657 fossil organisms recovered from bed 0, only 0·02 per cent belong to terrestrial groups (millipeds, arthropleurids, insects).

TABLE 1. Faunal composition of the Saint-Louis opencast pit as a whole, and for beds 0 and +2 (see Text-fig. 1B); N, number of concretions containing animal remains (complete specimens or identifiable remains); after unpublished data base (D. Sotty, pers. comm. 1999).

		Saint-Louis Total N = 10463	Saint-Louis Bed 0 N = 1657	Saint-Louis Bed +2 N = 569
Annelids		397 (3·8 %)	60 (3·6%)	36 (6·32%)
Onychophorans		5	–	–
Merostomes	Xiphosurids	142 (1·35 %)	17 (1·02%)	1
Arachnids	Scorpionids	6	–	–
	Spiders	26 (0·002%)	–	–
Crustaceans	Conchostracans	326 (3·11%)	3 (0·002%)	24 (4·21%)
	Ostracods	49 (0·004%)	5 (0·003%)	3 (0·005%)
	Phyllocarids	5	1	–
	Syncarids	5217 (49·86%)	804 (48·52%)	287 (50·43%)
	Isopods	12 (0·001%)	5 (0·003%)	–
Euthycarcinoids		111 (1·06%)	4 (0·002%)	17 (2·98%)
Myriapods		66 (0·006%)	6 (0·003%)	–
Arthropleurids		8	1	–
Insects		227 (2·17 %)	29 (1·75%)	–
Bivalves		2713 (25·92%)	717 (43·27%)	–
Amphibians		1048 (10·01%)	2 (0·001%)	198 (34·79%)
Agnathans		11 (0·001%)	–	2
Fishes		94 (0·09%)	3 (0·002%)	1

Ecological niche of Alanops *and other Carboniferous xiphosurans*

The xiphosuran diversity at Montceau is very low (only one species) in comparison with other Carboniferous biotas. For example, four xiphosuran genera (*Bellinurus*, *Euproops*, *Liomesaspis*, and *Valoisella*) are known to occur at Bickershaw (Westphalian A, Lancashire, UK; Anderson *et al*. 1997), and even five [*Euproops*, *Pringlia*, *Streptocyclus* (probably an invalid synonym), *Liomesaspis* and *Palaeolimulus*] in the Mazon Creek Lagerstätte (Westphalian D equivalent; see Mikulic *in* Shabica and Hay 1997, pp. 134–139). At Mazon Creek, xiphosurans are found mainly in the non-marine Braidwood facies (98 specimens; 0·3 per cent of fossiliferous concretions) except for *Paleolimulus* which is restricted to the marine Essex facies (nine specimens; 0·011 per cent of fossiliferous concretions) (Baird 1997*a*, *b*; Baird and Anderson *in* Shabica and Hay 1997, pp. 24–29). This clearly indicates that many Carboniferous xiphosurans had ecological preferences for freshwater environments.

Several lines of evidence (faunal associates, depositional environment, taphonomy, concretion mineralogy) suggest that *Alanops* lived in fresh water, in common with the non-marine Braidwood xiphosurans from Mazon Creek. However its exact ecological niche remains uncertain (streams, lakes, temporary water bodies, or the upper section of estuaries?).

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