

# SYNCARID CRUSTACEANS FROM THE MONTCEAU LAGERSTÄTTE (UPPER CARBONIFEROUS; FRANCE)

by VINCENT PERRIER\*, JEAN VANNIER\*, PATRICK R. RACHEBOEUF†, SYLVAIN CHARBONNIER\*, DOMINIQUE CHABARD‡ and DANIEL SOTTY‡

\*Université Claude Bernard Lyon 1, UMR 5125 PEPS 'Paléoenvironnements et Paléobiosphère', Campus scientifique de la Doua, Bâtiment Géode, 2 rue Raphaël Dubois, 69622 Villeurbanne, France; e-mails: vincent.perrier@univ-lyon1.fr; jean.vannier@univ-lyon1.fr

†Université de Bretagne Occidentale, UMR 6538 'Domaines Océaniques' – Paléontologie, UFR Sciences et Techniques, 6 avenue Le Gorgeu, CS 93837, F-29238 Brest cedex 3, France; e-mail: patrick.racheboeuf@univ-brest.fr

‡Musée d'Histoire Naturelle d'Autun, 14 rue St-Antoine, 71400 Autun, France

Typescript received 28 September 2004; accepted in revised form 17 May 2005

**Abstract:** Key aspects of the morphology, autecology, systematics and taphonomy of the crustacean syncarids from the Montceau Lagerstätte (Upper Carboniferous, Stephanian B; France) are presented. *Palaeocaris secretanae* is the most abundant faunal element of the Montceau biota and shows striking morphological similarities with *Palaeocaris typus* from the Mazon Creek Lagerstätte (Westphalian D; Illinois, USA). *Palaeocaris secretanae* was a shrimp-like animal with a short head (no head shield), large mandibles, 14 trunk segments (the first one being reduced) and a fan-like caudal termination. Both the body and the appendage design indicate abilities for crawling on the substratum (slender endopods) and for escape reaction (uropodal fan, pleonal flexibility), although swimming activities may have been reduced (trunk appendages with small flap-like exopods). Details of the appendages involved in feeding, e.g. mandibles and maxillipeds, indicate poor ability for predation but point to an omnivorous detritus feeding mode. Poorly developed respiratory organs (small cylindrical epipods)

suggest a relatively low level of locomotory activity. The field of vision may have been large and panoramic (stalked eyes). Rows of pores on 12 trunk segments are interpreted as possible sensory organs used for current detection. Females were brooding eggs (clusters of eggs preserved along anteroventral trunk). Microprobe analysis indicates that siderite is the major component of the nodules. Four events played a key-role in the three-dimensional preservation of syncarids: (1) rapid burial, (2) minimal decomposition, (3) phosphatic mineralization shortly after the animal's death and (4) nodule formation around the carcass. *Palaeocaris secretanae* is morphologically close to Recent syncarids such as *Anaspides tasmaniae* (freshwater streams, Australia) in its general body plan and detailed anatomy, e.g. mouth parts, indicating morphological stasis in syncarids over more than 200 million years.

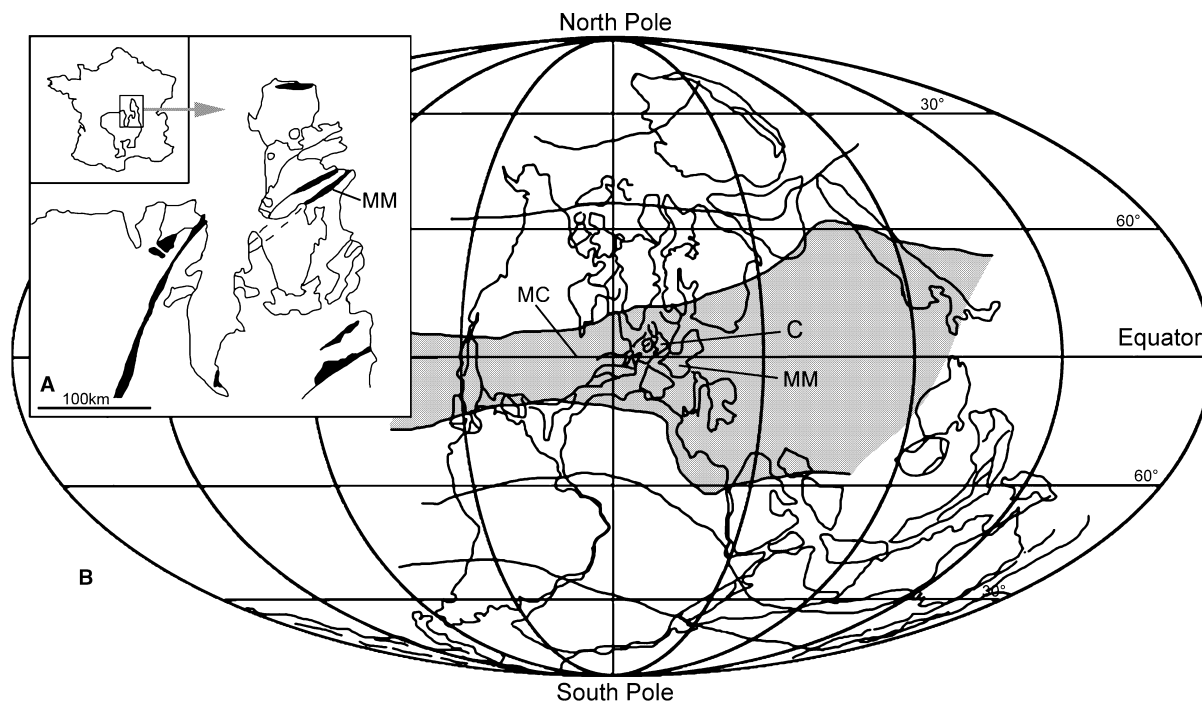
**Key words:** syncarids, crustaceans, Lagerstätte, taphonomy, Montceau-les-Mines, Upper Carboniferous.

SYNCARIDS are shrimp-like crustaceans that live in a variety of freshwater aquatic environments such as streams and lakes, e.g. *Anaspides tasmaniae*. The majority of the present-day species have colonized interstitial niches and underwent considerable reduction in size as an adaptive response to their lifestyle. Palaeontological studies (see Schram 1984 for references) indicate that the early ancestors of the group were probably marine (Schram 1981; Briggs *et al.* 1991) but information is sparse concerning the Palaeozoic evolution of the group and its ecological shift from marine to freshwater habitats. The Carboniferous seems to have been a key period in the ecological diversification of syncarids. The Montceau Lagerstätte (Text-fig. 1), in which syncarids are extremely abundant, provides a unique opportunity to study the anatomy, autecology and ecological preferences of the group during the Late Carboniferous (Stephanian). Moreover, the excellent

quality of preservation of the fossil specimens allows unprecedentedly detailed, three-dimensional reconstructions of the external anatomy of *Palaeocaris secretanae*, the only syncarid found at Montceau. New interpretations concerning the autecology of *P. secretanae* are also proposed, supported by comparisons with non-interstitial Recent syncarids such as *Anaspides tasmaniae*.

## GEOLOGICAL SETTING

The Blanzy-Montceau-les-Mines Basin is located in the north-eastern part of the Central Massif (France; Text-fig. 1) and belongs to the Variscan tectonic complex that extended across Europe during the Carboniferous Period. Sedimentation in the Montceau Basin started during the Late Stephanian (the Early Stephanian not represented)



**TEXT-FIG. 1.** Location of the Montceau Lagerstätte (Upper Carboniferous, France). A, sketch map of the north-eastern part of the Massif Central showing main Carboniferous basins (modified after Poplin 1994, fig. 3). B, world map for the Upper Carboniferous (Scotese and McKerrow 1990); the Montceau-les-Mines (MM; France), Mazon Creek (MC; Illinois, USA) and Coseley (C; Worcestershire, UK) Lagerstätten all lie within the tropical zone (grey area).

and continued through to the Permian. The sedimentation is typically that of a graben with fluvio-lacustrine clastics deposited under tropical conditions. Nodules were found in the mudstones of the Assise de Montceau at the top of the first coal layer. This horizon (thickness *c.* 30 m), rich in nodules, was exposed in four opencast mines that yielded abundant fossiliferous nodules over the years, namely, the St-Louis (over 100,000 nodules with either plant or animal remains), La Sormes St-Hélène and St-François (only plant remains) opencast mines (Sotty 1980). These four mines were filled up or flooded after the coal exploitation ended in the 1980s and are no longer accessible.

The age of the nodule layers (Late Stephanian) is based on the composition of the plant assemblages that comprise Lycophyta, Sphenophyta, Pteridophylla (Filicophyta) and Cordaitophyta (Doubringer 1994; Langiaux 1994).

## MATERIAL AND METHODS

### *Fossil material*

The syncarids from Montceau are preserved in sideritic nodules (long axis 2–5 cm) and were not found in the surrounding matrix (bioclastic peloidal mudstones). Each nodule typically contains a single syncarid (Text-fig. 2A–B) that lies in the centre of the concretion. Only one

flattened and rather shapeless nodule yielded an assemblage of three small, complete syncarids (Text-fig. 2C). Nodules were split open with a hammer and yielded a majority of complete specimens (body length between 10 and 30 mm), some of them with excellently preserved appendages and eggs. Approximately 5244 syncarid-bearing concretions registered in the database of Sotty's collection (Autun) were collected from St-Louis opencast by D. Sotty and his co-workers during successive field excursions from 1979 to 1983. Only 286 specimens were selected for the present study. The remaining material is poorly preserved and provides no additional information relevant to the morphology of *Palaeocaris secretanae*. All of the material is in the D. Sotty collection, and belongs to the Museum National d'Histoire Naturelle de Paris (MNHN-SOT numbers). It is deposited in the Museum d'Histoire Naturelle, 14 rue St-Antoine, F-75140 Autun (Chabard and Poplin 1999).

Comparative material was obtained from: (1) The Illinois State Museum (Springfield, Illinois, USA; ISM numbers): five specimens of *Palaeocaris typus* Meek and Worthen, 1865 from Mazon Creek (ISM.14833, 14842, 14845, 14846, 14849); (2) The Field Museum of Natural History (Chicago, Illinois, USA; PE numbers): three specimens of *Palaeocaris typus* Meek and Worthen, 1865 from Mazon Creek (PE.23237, 37957, 37976); (3) The Geological Survey Museum (Nottingham, UK; GSM numbers):



**TEXT-FIG. 2.** Photographs of nodules yielding *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France. A, MNHN-SOT 96571a, lateral view;  $\times 1.7$ . B, MNHN-SOT 9667a, lateral view;  $\times 3$ . C, MNHN-SOT 23128a, three specimens in lateral view;  $\times 2$ .

two specimens of *Palaeocaris retractata* Calman, 1932 from the British Coal Measures (GSM.26720, 26721); (4) The Natural History Museum (London, UK; I and In numbers): ten specimens of *Palaeocaris retractata* Calman, 1932 from the British Coal Measures (I.13971, 15912; In. 29012, 29013, 29014, 29017, 29024, 62047, 62048, 62049).

The syncarids were examined under the binocular microscope and camera-lucida drawings were made (complete specimens and anatomical details). Some specimens had to be carefully prepared using small needles. Latex casts were made from some external moulds. Fine anatomical features, e.g. feeding appendages and sensory pores, were studied under the scanning electron microscope (Hitachi SEM S800). Taphonomic aspects of syncarids were studied by using microprobe analysis (CAMECA Camebax, UMR 5570 UCB Lyon1).

*Recent material*

*Anaspides tasmaniae* Thompson, 1893 (pl. 1) and *Koonunga* sp. were obtained from the Armidale University, New South Wales, Australia (courtesy A. Boulton). These two species were collected on the gravel bottom of streams in New South Wales (Boulton and Foster 1998) and were preserved in 70 per cent alcohol. Complete and dissected specimens were observed under the binocular microscope and the SEM after being desiccated using hexamethyldisilazane following the method of Felgenhauer (1987).

**FOSSIL AND RECENT SYNCARIDS: PREVIOUS WORK**

Syncarids were first described as fossils (*Uronectes fimbriatus* Jordan, 1847) before living representatives of the group were discovered in the mountain streams of Tasmania (Thompson 1893). The first detailed descriptions of fossil taxa were made by Meek and Worthen (1865;

*Acanthotelson stimpsoni* and *Palaeocaris typus*). Packard (1885) erected the Syncarida as an order of Crustacea. The Palaeocaridacea, to which *Palaeocaris* belongs, was created by Brooks (1962).

The most recent review of syncarids is that of Schram (1984), who divided the group into three suborders: the Palaeocaridacea Brooks, 1962, the Anaspidae Calman, 1904, and the Bathynellacea Chappuis, 1915. His classification is based on two important characters: the number of articles in thoracic endopods (four in bathynellaceans, five in palaeocaridaceans and anaspidaeans) and the shape of the first thoracic segment (fused to the cephalon in anaspidaeans and free in palaeocaridacean and bathynellaceans).

*Palaeocaridacea (Dinantian–Lower Permian)*

The Palaeocaridacea was an important group during the Palaeozoic (23 species) and has a well-documented fossil record (see species list and references in Table 1) through the Carboniferous (France, England, Scotland, Ireland, Germany, the Netherlands, USA) and the Permian (France, Slovakia, Germany, North and South America). The oldest known palaeocaridacean is *Minicaris brandi* Schram, 1979 from the Granton shrimp-bed of Scotland (Lower Oil Shale Group, Dinantian; Carter 1987; Carter *et al.* 1989) deposited in possible interdistributary bay or deltaic environments (Briggs and Clarkson 1989; Briggs *et al.* 1991). There is no fossil record of palaeocaridaceans in rocks younger than the Early Permian, *Nectotelson krejci* Fritsch, 1875 (Nýřan near Pilsen, Czech Republic) being the last occurrence of the group. The palaeocaridaceans from Montceau were first described, succinctly, by Secrétan (1980a) before *Palaeocaris secretanae* was established by Schram (1984). Secrétan (1980b) also focused on the cephalic shield of *P. secretanae* and its evolutionary significance within the crustaceans. More recently, a preliminary study of the autecology and taphonomy of this species was made by Perrier (2003) and Perrier *et al.* (2003).

**TABLE 1.** Taxonomic checklist of fossil syncarids, after Schram (unpublished worksheet). For Schram and Chestnut (1984) see Schram (1984); for Uhl and Raisch (1999) see Uhl (1999); \*= type species.

Family	Genus	Species	Author, year	Age	Occurrence
Acanthotelsonidae	<i>Acanthotelson</i>	<i>stimpsoni</i> *	Meek and Worthen, 1865	M. Pennsylvanian	USA (Illinois, Indiana)
		<i>kentuckiensis</i>	Schram and Chestnut, 1984	M. Pennsylvanian	USA (Kentucky)
	<i>Palaeosyncaris</i>	<i>dakotensis</i> *	Brooks, 1962	U. Mississippian	USA (North Dakota)
		<i>micra</i>	Schram, 1984	M. Pennsylvanian	USA (Illinois, Indiana)
	<i>Uronectes</i>	<i>fimbriatus</i> *	(Jordan, 1847)	L. Permian	Germany
		<i>kinniensis</i>	Schram and Schram, 1979	Pennsylvanian	USA (New Mexico)
<i>palatinus</i>		Uhl and Raisch, 1999	U. Carboniferous	Germany	
Minicarididae	<i>Minicaris</i>	<i>brandi</i>	Schram, 1979	L. Carboniferous	Scotland
	<i>Erythrogaulos</i>	<i>carrizoensis</i>	Schram, 1984	L. Permian	USA (New Mexico)
Palaeocarididae	<i>Monicaris</i>	<i>rudnicensis</i>	Stamberg, 2000	L. Permian	Czech Republic
		<i>Palaeocaris</i>	<i>retractata</i>	Calman, 1932	U. Carboniferous
		<i>secretanae</i>	Schram, 1984	U. Carboniferous	France
		<i>typus</i> *	Meek and Worthen, 1865	M. Pennsylvanian	USA (Illinois, Indiana)
Squillitidae	<i>Nectotelson</i>	<i>krejci</i>	(Fritsch, 1875)	L. Permian	Czech Republic, France
	<i>Praeanaspides</i>	<i>praeacursor</i>	Woodward, 1908	U. Carboniferous	UK
	<i>Squillites</i>	<i>spinus</i>	Scott, 1938	U. Mississippian	USA (Montana)
uncertain fam.	<i>Brooksycaris</i>	<i>canadensis</i>	Brooks, 1962	U. Carboniferous	USA (Nova Scotia)
	<i>Clarkecaris</i>	<i>brasilius</i>	(Clarke, 1920)	Permian	Brazil
	<i>Palaeoarchestia</i>	<i>parallela</i>	(Fritsch, 1876)	L. Permian	Czech Republic
	<i>Pleurocaris</i>	<i>annulatus</i> *	Calman, 1911	U. Carboniferous	UK, France
		<i>juengeri</i>	Schöllmann, 1999	U. Carboniferous	Germany
	<i>Spinocaris</i>	<i>horribilis</i>	Uhl, 1999	U. Carboniferous	Germany
	<i>Williamocalmania</i>	<i>vandergrachtii</i>	(Pruvost, 1922)	L. Carboniferous	Netherlands
Anaspididae	<i>Anaspidites</i>	<i>antiquus</i>	(Chilton, 1929)	Triassic	Australia (NSW)
	<i>Koonaspides</i>	<i>indistinctus</i>	Jell and Duncan, 1986	Cretaceous	Australia (Victoria)

*Anaspidacea (Triassic–Recent)*

Anaspidaceans are known from the Triassic, e.g. *Anaspides antiquus* (Chilton, 1929) from the freshwater (Jones and Rust 1983) Hawksbury Sandstone, New South Wales, Australia (Brooks 1962; Schram 1984), the Cretaceous, e.g. *Koonaspides indistinctus* Jell and Duncan, 1986 from Koonawara, New South Wales, Australia (Jell and Duncan 1986), through to the Recent. Recent anaspidaceans (Pl. 1) consist of a few tens of species all living in freshwater environments, e.g. coarse bottom sediment of mountain streams and lakes, of Australia and Tasmania (Boulton and Foster 1998). Anaspidaceans and palaeocaridaceans have the same overall morphology (body plan, appendage design) and size

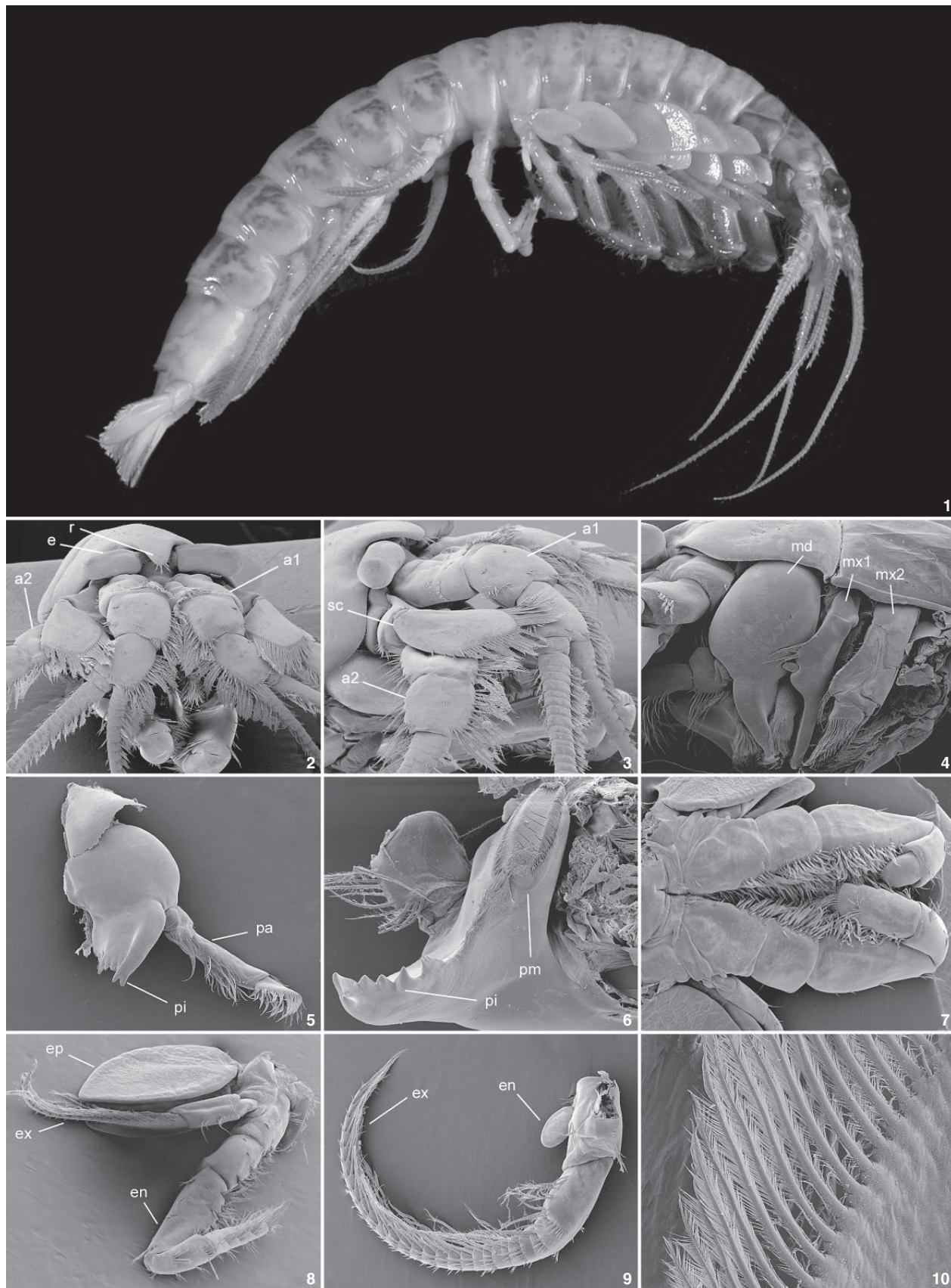
range and may have had the same ecological preferences for freshwater environments. It is envisaged that anaspidaceans evolved from the palaeocaridacean stock during the Palaeozoic–Mesozoic transition (Schmincke 1978).

*Bathynellacea (Recent)*

The Bathynellacea have no fossil record. It is a very successful group of syncarids that occupies freshwater continental stream beds or caves, or marine beach sand environments on virtually all continents (not Antarctica) at almost all latitudes (60°N–60°S; Coineau 1996). Despite numerous adaptive features in direct relation to

**EXPLANATION OF PLATE 1**

Figs 1–10. Syncarid *Anaspides tasmaniae* (Thompson, 1904) from New South Wales (Australia). All scanning electron micrographs except (1). 1, adult specimen in lateral view; × 5. 2, cephalon showing lateral eyes (e), rostrum (r), antennules (a1) and antennae (a2) in frontal view; × 16. 3, anterior part of the cephalon showing a1 and a2 (bearing scaphocerite, sc) in lateral view; × 20. 4, feeding appendages, from left to right: mandible (md), maxillule (Mx1) and maxilla (Mx2) (basal parts concealed under cephalic shield) in lateral view; × 20. 5, dissected mandible showing palp (pa) and processus incisivus (pi) in lateral view; × 20. 6, mandible showing processus incisivus and processus molaris (pm) in ventral view; × 40. 7, maxillipeds in ventral view; × 13. 8, dissected left thoracic appendage showing the two epipods (ep), the exopod (ex) and the endopod (en) in lateral view; × 15. 9, pleopod showing the reduced endopod and the long multi-articulated and setose exopod in lateral view; × 15. 10, uropod setae in dorsal view; × 75.



their interstitial lifestyle (size below 2 mm, loss of eyes, uropod and telson not as a fan-like structure), bathynellaceans still possess the major diagnostic features of syncarids, e.g. lack of carapace, all thoracic segments free.

Schram (1984) discussed the phylogeny of Syncarida based on cladistic analysis. Useful information concerning the biology and systematics of syncarids can be found in Coineau (1996) and Lopretto and Morrone (1998).

## SYSTEMATIC PALAEOLOGY

*Morphological terms.* The following abbreviations are used on the text-figures and plates: a1, first antenna; a2, second antenna; ce, cephalon; cs, cephalic shield; dt, digestive tract; e, eyes; eg, eggs; en, endopod; ep, epipod; ex, exopod; fg, flagellum; lb, labrum; md, mandible; mg, mandibular groove; Mx1, maxilla (first pair); Mx2, maxilla (second pair); Mxp, maxilliped; pa, palp; pi, processus incisivus; pl, pleon; pl1–5, pleopods (first to fifth pair); pm, processus molaris; ps1–6, pleonal segments (first to sixth); r, rostrum; sc, scaphocerite; t, telson; th, thorax; th1–8, thoracic segments (first to eighth); u, uropod.

Superclass CRUSTACEA Linnaeus, 1758

Class MALACOSTRACA Latreille, 1805

Subclass EUMALACOSTRACA Grobden, 1892

Superorder SYNCARIDA Packard, 1885

*Diagnosis* (after Rupert and Barnes 1994, modified). Eumalacostracans that lack a carapace; all thoracic segments free or the first fused with the head; at least some thoracic appendages biramous, eighth pair often reduced (Recent species); telson with uropods.

Order PALAEOCARIDACEA Brooks, 1962

*Diagnosis* (after Schram 1986, modified). Syncarids with first thoracic segment not fused to the cephalon, although frequently reduced; A2 endopod modified into a scaphocerite (scale-like feature); first thoracopod typically reduced and modified as a maxilliped; all thoracic appendages similarly orientated; endopods of thoracic segments with five components; tail developed as a fan-like structure (strong lobate uropods); exopod of uropods usually with diaeresis (axial cuticular thickening).

Family PALAEOCARIDIDAE Meek and Worthen, 1865

*Diagnosis* (after Schram 1984, modified). Palaeocaridaceans with thoracic appendages bearing leaf-like exopods. Pleopods with multi-articulated exopods and endopods.

Genus PALAEOCARIS Meek and Worthen, 1865

*Type species.* *Palaeocaris typus* Meek and Worthen, 1865 from the Pennsylvanian of Mazon Creek, Will County, Illinois, USA; also occurs in the Lower Shelburn Formation of Indiana, and at Windsor, Missouri, USA (Schram 1984).

*Other species.* *Palaeocaris secretanae* Schram, 1984 from the Stephanian of Montceau-les-Mines, Saône et Loire, France, and *Palaeocaris retractata* Calman, 1932 from the Pennsylvanian of Dudley, Worcestershire and Lickey Hills, Warwickshire, UK (Schram 1984).

*Diagnosis* (after Schram 1984, modified). Palaeocarididae with large mandible (width *c.* 0.5 cephalic shield length). First thoracic segment strongly reduced. Sixth pleonal segment armed with two pointed posteroventral extensions. Paddle-like uropods (exopods longer than endopods) strengthened by central and peripheral ridges and bearing closely spaced setae and spines.

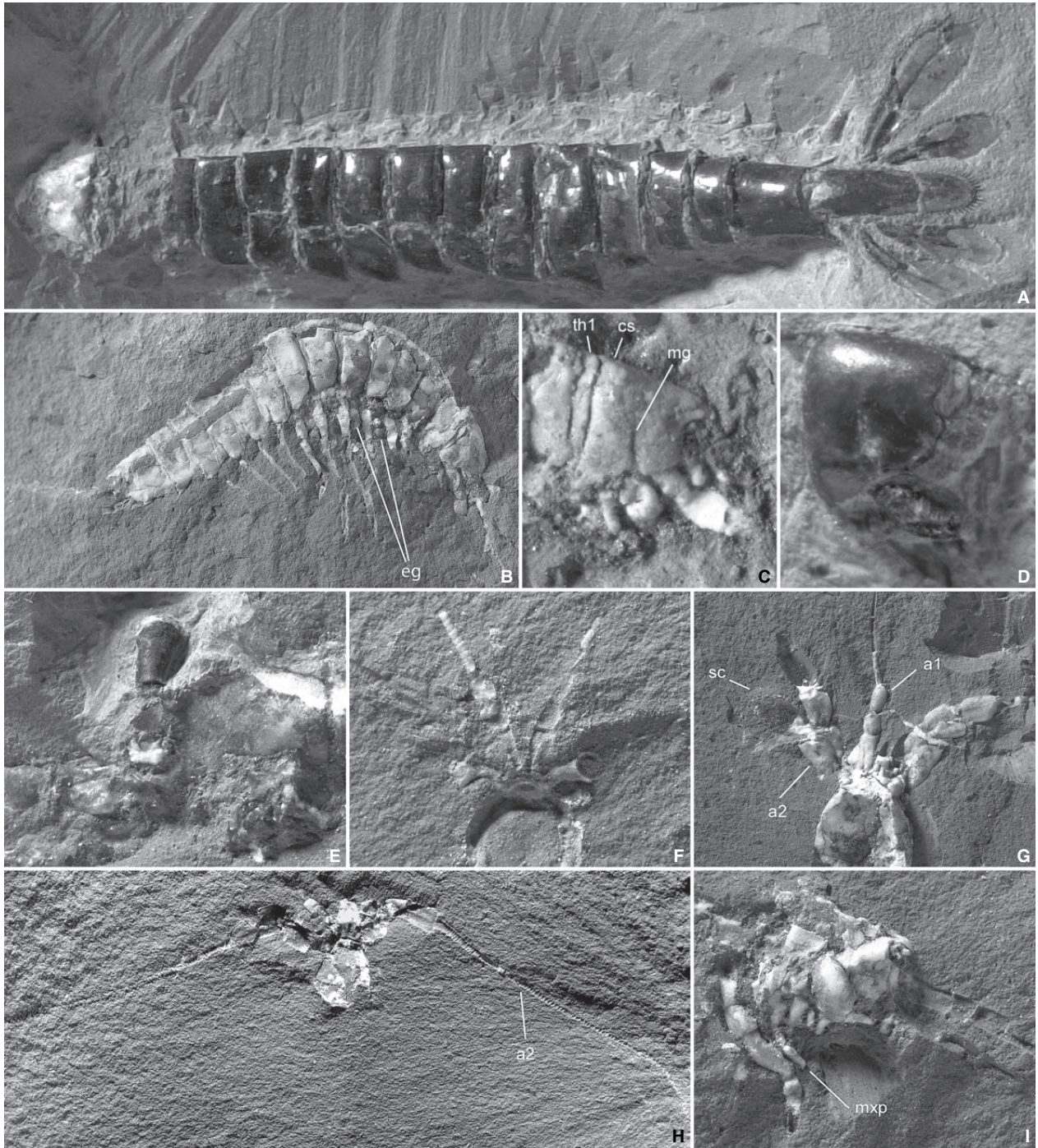
*Distribution.* *Palaeocaris* occurs in both Europe (UK, France) and North America (USA) and ranges from Moscovian (*Palaeocaris retractata*) through to the Kasimovian (*Palaeocaris secretanae*) (Benton 1993).

*Palaeocaris secretanae* Schram, 1984

Plate 2; Text-figures 2–6, 9, 12

- v. 1980a palaeocarid syncarid; Secrétan, p. 24, pl. 1.
- v. 1980a ?ceratiocarid phyllocarid; Secrétan, p. 28, pl. 2, figs 1–2.
- v. 1980a ?eocaridacean; Secrétan, p. 28, pl. 3, figs 2–3.
- v. 1980a pygocephalomorph; Secrétan, p. 30, pl. 3, figs 5–6.
- v. 1980a ?palaeostomatopod; Secrétan, p. 30.
- v. 1980a 'spécimens énigmatiques'; Secrétan, p. 32, pl. 4, figs 2, 6.
- 1980b *Palaeocaris* sp.; Secrétan, p. 414, pls 1–4, fig. 1.
- 1981 *Palaeocaris* cf. *P. retractata* Calman; Pacaud *et al.*, p. 40.
- 1982 *Palaeocaris* cf. *P. retractata* Calman; Rolfe *et al.*, p. 426.
- 1984 *Palaeocaris secretanae* Schram, p. 221, fig. 17; p. 223, pl. 6, figs B–F; p. 224, pl. 7, figs A–B.
- 1994 *Palaeocaris secretanae* Schram; Schram and Secrétan, pp. 157–159, figs 1A, 2–4.
- 2003 *Palaeocaris secretanae* Schram; Perrier, p. 5, fig. 3; p. 8, figs 5–8; p. 9, fig. 9; p. 17, fig. 11; p. 21, fig. 14; p. 24, figs 16–17; pp. 45–52, pls 1–8.

*Holotype.* MNHN-SOT 3674a, b: part and counterpart of a complete specimen preserved laterally, from the St-Louis opencast mine, north of Montceau-les-Mines (Saône et Loire, France),



**TEXT-FIG. 3.** Photographs of the general morphology of *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France. A, MNHN-SOT 5795a, dorsal view showing complete trunk and tail fan;  $\times 10$ . B, MNHN-SOT 24746a, lateral view of a complete specimen showing appendages and eggs (eg);  $\times 6$ . C, MNHN-SOT 3686a, detailed lateral view showing the cephalic shield (cs) incised by the mandibular groove (mg) and followed by the first, strongly reduced, thoracic segment (th1);  $\times 12$ . D, MNHN-SOT 3689a, lateral view of the cephalic shield preserved in 3D;  $\times 13$ . E, MNHN-SOT 78506a, lateral view of the cephalic shield showing the bulb-like eye peduncle;  $\times 15$ . F, MNHN-SOT 9072b, dorsal view of the cephalic shield showing eyes and first antennae;  $\times 10$ . G, MNHN-SOT 82097a, dorsal view of the cephalic shield showing a1 and a2 bearing scaphocerite (sc);  $\times 8$ . H, MNHN-SOT 5293a, dorsal view of the cephalic shield showing a2 multi-annulated flagella;  $\times 6$ . I, MNHN-SOT 5737a, lateral view of the cephalic shield showing maxilliped (mxp) in front of second thoracic appendage;  $\times 10$ . All light photographs.

Assise de Montceau, bed +2; Stephanian B (Babin 1994; Doubinger 1994; Langiaux 1994).

*Paratypes.* Two specimens from the same locality are designated here as paratypes: MNHN 5795a, b preserved in dorsal view (Pl. 2, figs 6–12; Text-figs 3A, 4E, 6A, 13A–B) and MNHN 24746a, b (Text-figs 3B, 6C) a complete specimen preserved laterally. Both provide important information on the morphology of *Palaeocaris secretanae* and on its possible life attitude.

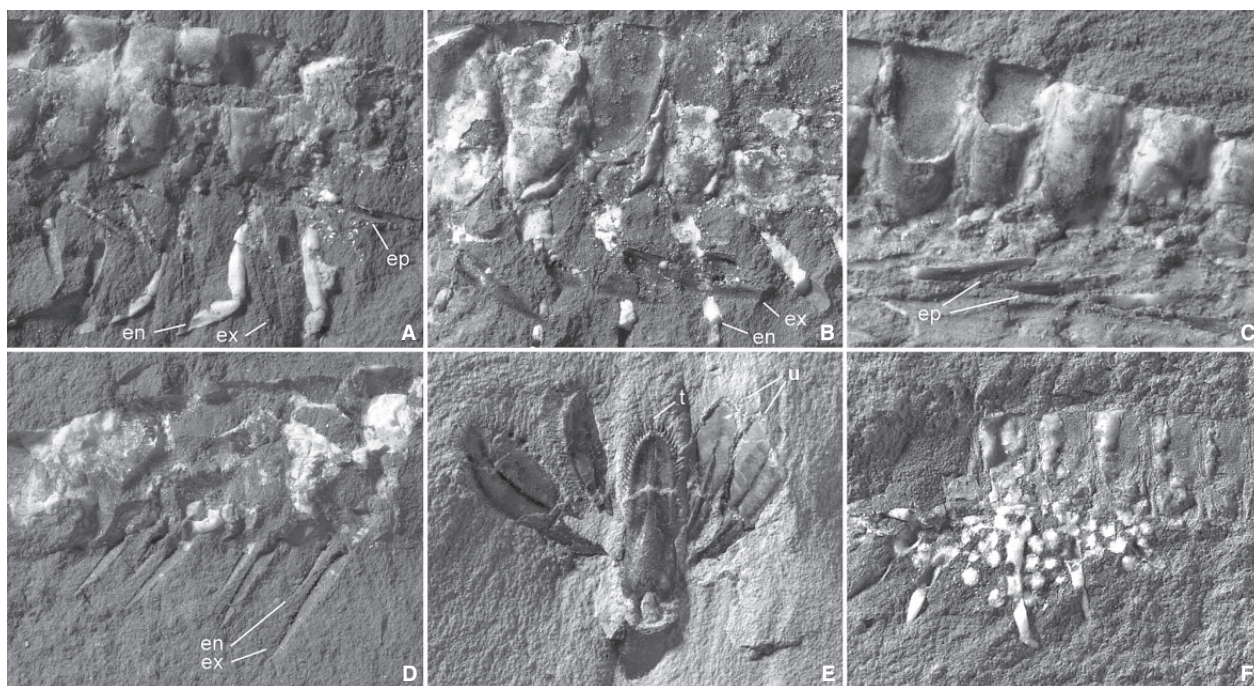
*Material.* At least 5244 specimens (1300 excellent) all preserved in sideritic nodules. Most of these specimens are from bed 0 and bed +2 of the St-Louis open-cast mine (Pacaud and Sotty 1994).

*Diagnosis* (after Schram 1984, modified). *Palaeocaris* with smooth triangular cephalic shield (length *c.* 0.25 thorax length). Basal part of A1 with three segments (articles), almost as long as the unit formed by the protopod and the first endopodal segment of A2. A1 with scaphocerite almost as long as the two first segments of A2 endopod. All thoracic segments of similar size, trapezoidal shape in lateral view except first segment (*c.* 0.75 narrower than other segments). Pleonal segments all similar in shape but decreasing in size posteriorly. Telson slender, subelliptical in dorsal view, fringed with strong spines and bearing a long axial ridge.

### Description

*Cephalon.* The cephalic shield has a triangular outline in lateral view and a short, pointed rostrum that overhangs a deep notch through which each stalked eye protrudes (eye socket). Cuticular thickenings are present along its anterior and ventral margins. The cephalic shield is incised by a median groove at the level of the mandible (deeper ventrally, see Text-fig. 3C–D; Pl. 2, fig. 1). No external ornament is visible (MNHN-SOT 3689a, 79401b).

Lateral eyes are large, pear-shaped and mounted on a conical stalk (max. 1 mm long; see Text-fig. 3E–F; Pl. 2, fig. 2) (MNHN-SOT 78506a, 9072b, 97072b). The basal part of A1 consists of three components (first one broad-based with a triangular outline), which are fringed with marginal setae (length, diameter and spacing, 250, 15 and 30  $\mu\text{m}$ , respectively). Both the endopod and the exopod of A1 extend into a long flagellum (basal diameter 200  $\mu\text{m}$ ; see Text-figs 3F–G, 5C–D). The exact length of flagella is often impossible to determine due to the oblique burial of the animal (MNHN-SOT 5293a, 82079b, 79401b). A2 has a strong quadrangular protopod fringed with setae and bears a spine along its outer anterior margin. The exopod is represented by a small scale-like scaphocerite with closely spaced setae along its entire margin (length, diameter and spacing, 300, 15 and 15  $\mu\text{m}$ , respectively). The two basal components of the endopod are strong, subquadrangular and setose (inner margin of the second component pointed), and are followed by an extremely long, multi-articulated flagellum



**TEXT-FIG. 4.** Photographs of the appendages of *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France. A, MNHN-SOT 96577b, lateral view showing thoracic appendages with leg-like endopod (en), blade-shaped exopod (ex) and epipod (ep);  $\times 12$ . B, MNHN-SOT 79377, lateral view of thoracic appendages;  $\times 10$ . C, MNHN-SOT 3683a, lateral view of thorax showing folded back epipodites;  $\times 9$ . D, MNHN-SOT 89302b, lateral view of the pleonal biramous appendages (pleopods);  $\times 11$ . E, MNHN-SOT 5795a, dorsal view of the tail fan, showing telson flanked by paddle-like uropods;  $\times 9$ . F, MNHN-SOT 5736a, lateral view showing clusters of eggs between thoracic appendages;  $\times 10$ . All light photographs.



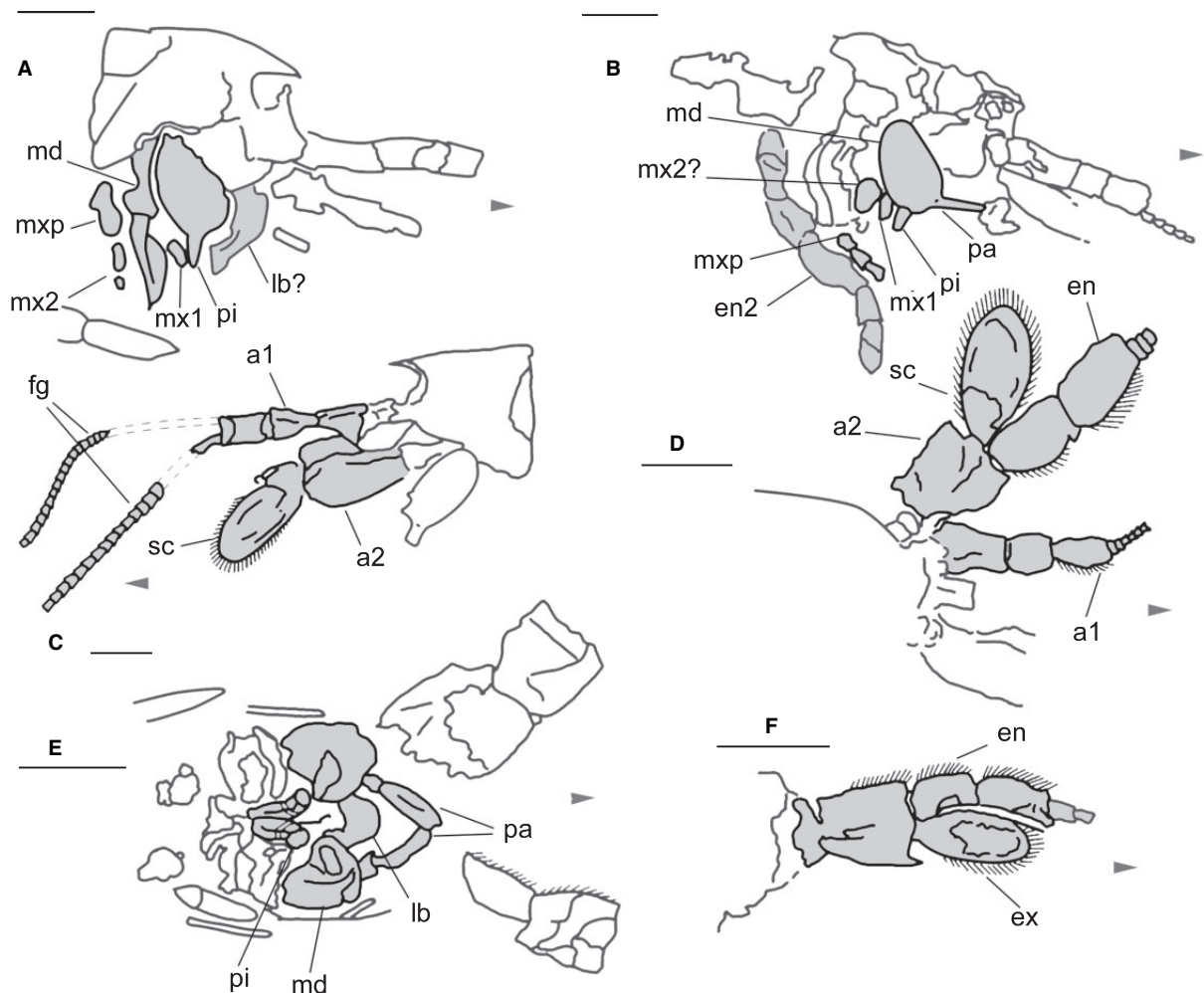
(diameter near base 400  $\mu\text{m}$ ; see Text-figs 3G–H, 5C–D, F; Pl. 2, figs 3–4). The length of the flagellum may reach at least half the length of the whole animal; it is typically recurved posteriorly (MNHN-SOT 82079b, 82097ab, 89302a, 84850ac).

The labrum is well exposed in MNHN-SOT 101704a and has a trapezoidal shape (Text-fig. 5E); it lies between and slightly above the attachment area of mandibles where the mouth opened.

The mandible is by far the most prominent part of the feeding apparatus, although its upper part is often concealed beneath the head shield. It has a swollen ovoid shape and is often preserved in three dimensions (Text-figs 3I, 5A–B; Pl. 2, fig. 5). It bears a well-developed palp (at least two articles) pointing anteriorly and an incisor process directed posteroventrally and towards the ventral groove of the animal. The molar process is present but its detailed morphology is unknown. However, several specimens (MNHN-SOT 7444a, 100104b, 519b, 5737a,

99689c, 73813a, 101704a) exposed in ventral view clearly show a pair of small, symmetrical, rectangular outgrowths along the inner side of the mandible (Text-fig. 12D). These features are interpreted as the molar processes of the mandibles. Mx1 is incompletely preserved (MNHN-SOT 7444a) and shows one segment that lies parallel to the axis of the incisor process. Mx2 is longer than Mx1 (see Text-fig. 5A; Pl. 2, fig. 5), and has the shape of a pointed knife whose blade is directed anteriorly and runs perpendicular to the longitudinal axis of the animal (MNHN-SOT 7444a, 519b).

*Trunk.* This consists of 14 (eight thoracic, six pleonal) segments (Text-figs 3A–B, 6A, C, 12A–B). Segments 2–13 are virtually uniform in shape and size (subquadrangular in dorsal view) although the pleonal segments gradually decrease in size posteriorly (Pl. 2, fig. 6). The first trunk segment is sharply reduced (length *c.* 0.3 of the length of the other segments,



**TEXT-FIG. 5.** *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France, camera lucida drawings (appendages emphasized with grey tone). A–B, MNHN-SOT 7444a (same as Pl. 2, fig. 5) and MNHN-SOT 5737 (same as Text-fig. 3I), feeding appendages in lateral view. C, MNHN-SOT 79401b, antennules and antennae in lateral view. D, MNHN-SOT 82097b (same as Text-fig. 3G and Pl. 2, figs 3–4), antennules and antennae in dorsal view. F, MNHN-SOT 84850a, detail of right antenna in dorsal view. E, MNHN-SOT 101704a, ventral view showing feeding appendages. Small arrows indicate front part. Scale bars represent 1 mm. Abbreviations as indicated in text.

in dorsal view; Text-fig. 3C). By contrast with recent syncarids such as *Anaspides* (Pl. 1, fig. 1), it is not fused to the cephalon but articulated to it. The last trunk segment has a more conical shape and extends into two pointed, ventral projections along the uropods (Text-fig. 6A; Pl. 2, fig. 9). The remaining segments (2–13) are interconnected by well-developed articular membranes and have strengthening features along their ventral margins. Pleonal segments differ from thoracic segments in having spiny posterior margins (spine diameter and spacing 100 and 200  $\mu\text{m}$ , respectively; Text-figs 6C–D, F; Pl. 2, figs 6–8). Rows of small pores (diameter and spacing 5 and 30  $\mu\text{m}$ , respectively) of possible sensory function are present in the anterior half of each segment (Text-fig. 13A–B) except in the first and fourth segments (MNHN-SOT 5795a, 5484a, 95664d, 3681a).

There are clearly two different groups of trunk appendages in *Palaeocaris secretanae*: long and leg-like, attached to the thorax, and shorter and multi-articulated, attached to the pleon. The first thoracic appendage is strongly reduced (Text-figs 3I, 5B) and consists of a three-segmented branch (possibly the endopod; the rest of the appendage is not preserved). It is interpreted as a maxilliped. Thoracopods 2–8 have exactly the same design. The coxa bears a long cylindrical epipod (Text-fig. 4A, C). The basis is strong. The exopod consists of at least two segments (proximal short and conical, distal larger; its length equals the width of a trunk segment), flap-like and setose (Text-fig. 4A–B). The endopod (Text-figs 3B, 4A, 6E) has five components: a short and robust ischium, a long merus, a medium-sized propodus and carpus, and a small dactylus (MNHN-SOT 3674a, 24746a, 98588b, 96557b, 76792a, 79377c, 3683a, 1986a).

The first five pleomeres display a uniform series of biramous pleopods (Text-figs 4D, 6D). Each pleopod consists of a strong protopod from which the almost identical, short, multi-articulated endopod (shorter) and exopod (longer) branch off. These are covered with small setae; the exact number of their components could not be determined. The pleopods are half as long as the thoracic endopods (MNHN-SOT 91735b, 89302b, 99693d).

*Telson and uropods.* The body of *Palaeocaris secretanae* ends up in a well-developed tail fan formed by the telson and the uropods (Text-figs 3A, 4E, 6A). The telson is elongate, robust and reinforced by strong medial and lateral ribs. Moreover, its margins are armed with about 50 spines (length, diameter and spacing 250, 40 and 50  $\mu\text{m}$ , respectively); the two spines

adjacent to the longitudinal axis of telson are reduced (about 125  $\mu\text{m}$ ; see Pl. 2, fig. 12).

The uropods are attached to the last pleonal segment and fan out from below the telson into four flap-like structures (Pl. 2, fig. 10). Their protopod, sometimes visible in dorsal view, is short and cylindrical. The endopod and the exopod have a similar lobate shape with a medial and outer ridge. The outer margin of the exopod is fringed with strong spines similar to the spines of the telson (max. length and diameter, 300 and 80  $\mu\text{m}$ , respectively), the rest of the margin bearing a dense array of long setae (Pl. 2, fig. 11). The endopod also bears the same type of setae (length, diameter and spacing, 500, 15 and 20  $\mu\text{m}$ , respectively) but lacks spines (MNHN-SOT 5795a, 9084ab, 99322c).

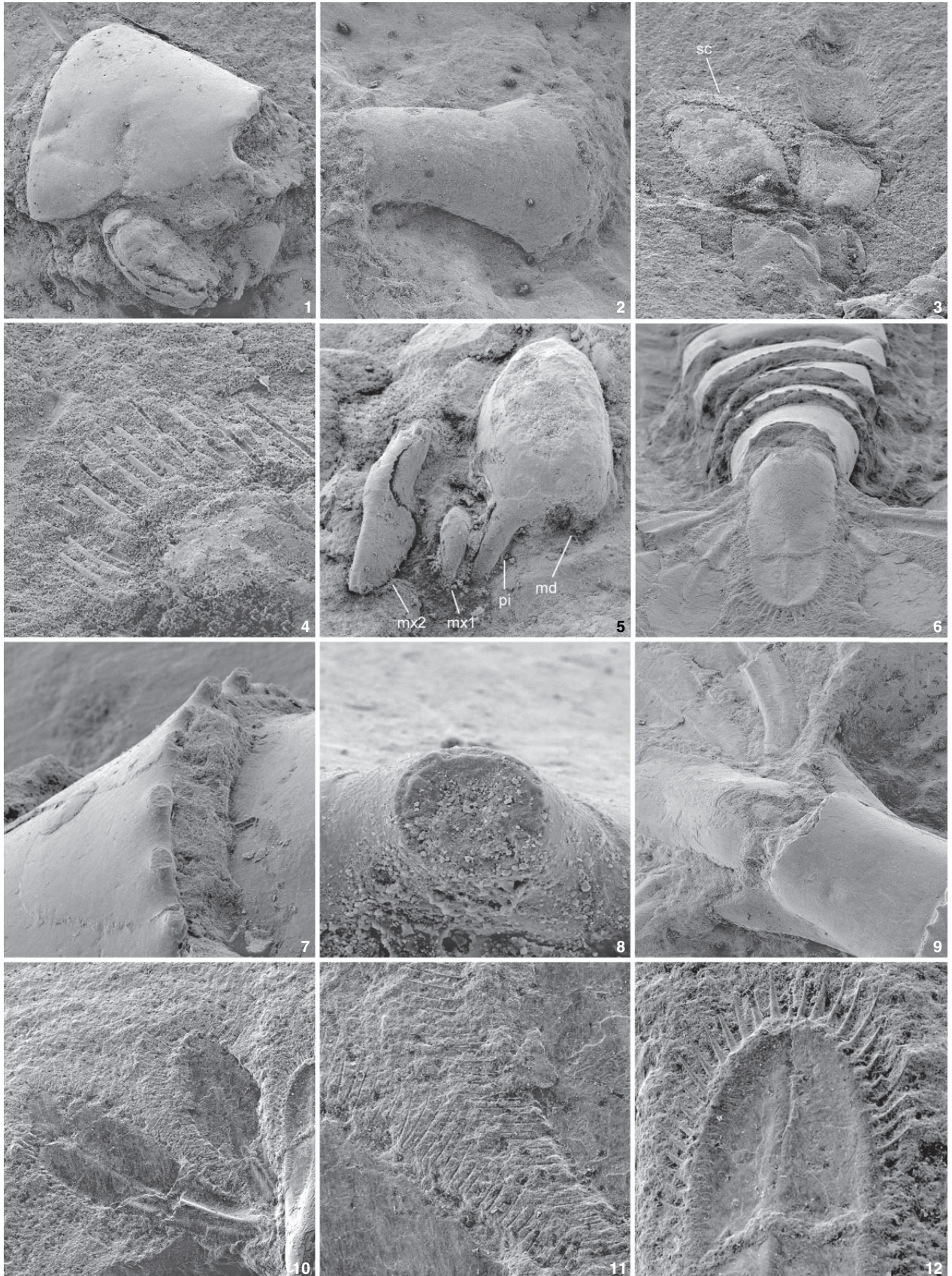
*Digestive tract.* The digestive tract of *Palaeocaris secretanae* is frequently preserved in three dimensions, and has a uniform cylindrical shape. It starts from behind the oesophagus (not preserved), runs parallel to the trunk axis of the animal and ends up (anus) along the ventral side of the telson (Text-fig. 6G). The digestive tract appears to be filled with mud rather than food remains. It resembles the gut of *Anaspides tasmaniae* that is similarly filled with mud. The surface of the gut of three specimens (MNHN-SOT 24746ab, 85449a, and 3019a) shows small wrinkles (Text-figs 3B, 6C).

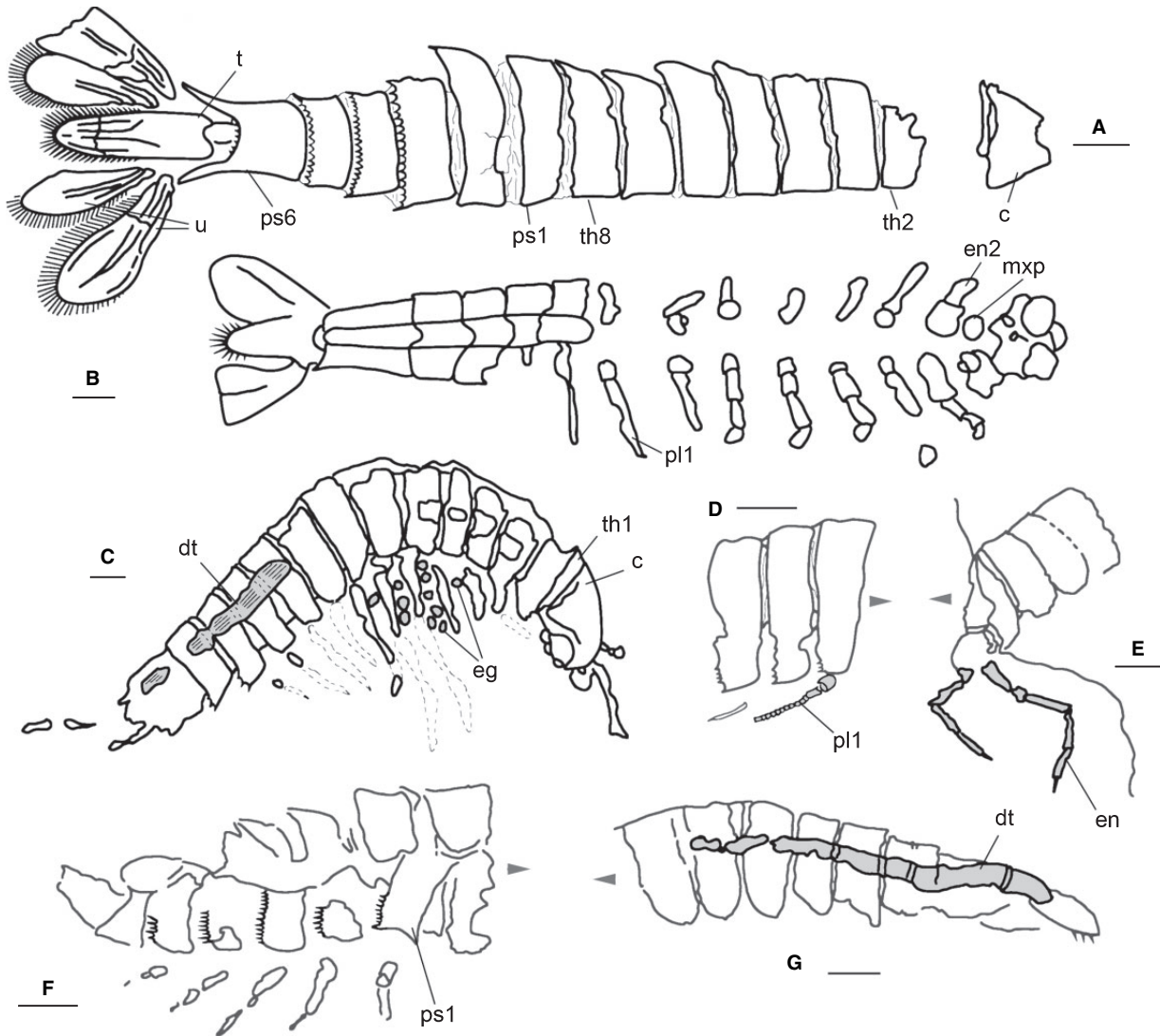
*Eggs.* Small spherical (300  $\mu\text{m}$  in diameter; Text-fig. 14C) features were observed between or close to the thoracic appendages of several specimens, and occasionally scattered in the surrounding matrix of nodules. The shape, size range and location of these features strongly suggest they may be eggs (MNHN-SOT 5736a, b; see Text-figs 3B, 4F, 6C). Indeed, some of these assumed eggs show a thin external layer (c. 30  $\mu\text{m}$ ) that could be interpreted as a protective capsule. There is often a gap between this layer and the egg infilling (white kaolinite). No ornament could be seen on the external surface of eggs. Egg-bearing specimens are most likely to be brooding females. Sexual dimorphism is not confirmed by size differences or external features between these assumed adult females (MNHN-SOT 5736ab, 15246a, 90444a, 95775abc, and 74685ab) and putative adult males.

*Distribution.* *Palaeocaris secretanae* is known only from the type locality.

## EXPLANATION OF PLATE 2

Figs 1–12. Detailed morphology of *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France. All scanning electron micrographs. 1, MNHN-SOT 3689a, cephalic shield with mandibular groove and underlying mandible in lateral view;  $\times 30$ . 2, MNHN-SOT78506a, eye peduncle (attachment, left) in dorsal view;  $\times 45$ . 3–4, MNHN-SOT 82097a, second antenna showing scaphocerite (sc) and details of scaphocerite tubular setae in dorsal view;  $\times 15$  and  $\times 120$ , respectively. 5, MNHN-SOT 7444, three-dimensionally preserved feeding appendages (compare with Pl. 1, fig. 4) from right to left: mandible (md) with processus incisivus (pi), maxillule (mx1) and maxilla (mx2) in lateral view;  $\times 43$ . 6–12, MNHN-SOT 5795a. 6, pleonal telescopic segments, telson and tail fan in posterodorsal view;  $\times 15$ . 7–8 strong spines along the posterodorsal margin of the fifth pleonal segment and detail of a broken spine (transverse section) in dorsal view;  $\times 80$  and  $\times 600$ , respectively. 9, sixth pleonal segment with two long spines pointing ventrally under the uropods in dorsal view;  $\times 20$ . 10–12, right uropods, details of uropod marginal setae and lobate telson in dorsal view;  $\times 15$ ,  $\times 50$  and  $\times 35$ , respectively.





**TEXT-FIG. 6.** *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France, camera lucida drawings (gut and some appendages emphasized with grey tone). A, MNHN-SOT 5795a (same as Text-figs 3A, 4E; Pl. 2, figs 6–12), paratype in dorsal view. B, MNHN-SOT 9045b, trunk appendages in ventral view. C, MNHN-SOT 24746a (same as Text-fig. 3B), complete specimen (paratype) with eggs between appendages in lateral view. D, MNHN-SOT 91735b, annulated pleopod in lateral view. E, MNHN-SOT 91735a, broken specimen showing a pair of thoracic endopods in transverse section. F, MNHN-SOT 5484a, pleonal segments bearing spines in lateral view. G, MNHN-SOT 85449a, digestive tract running parallel to pleon in lateral view. Small arrows indicate front part. Scale bars represent 1 mm. Abbreviations as indicated in text.

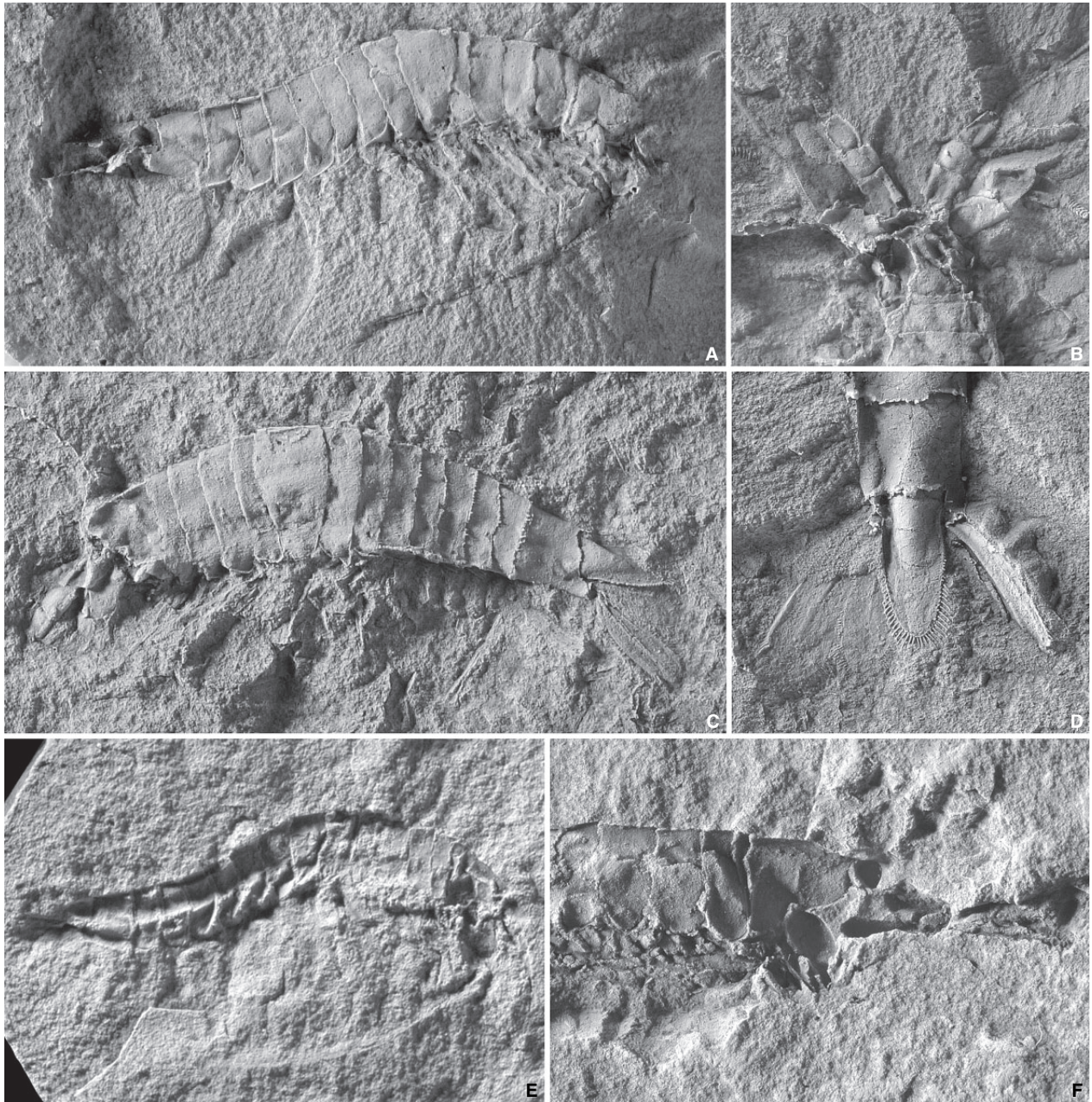
*Palaeocaris typus* Meek and Worthen, 1865  
Text-figures 7A–D, 8A–B

- 1984 *Palaeocaris typus* Meek and Worthen; Schram, p. 218, fig. 15; p. 219, pl. 5, figs A–C.  
1986 *Palaeocaris typus* Meek and Worthen; Schram, p. 88, fig. 7–1, B.  
1994 *Palaeocaris typus* Meek and Worthen; Schram and Secrétan, p. 156, fig. 1B.  
2003 *Palaeocaris typus* Meek and Worthen; Perrier, p. 21, figs 13–14; p. 56, pl. 6, figs C–D.

*Holotype.* Specimen X 338, University of Illinois, Paleontology Collections, Urbana, USA (Meek and Worthen 1865, fig. A, p. 552; Schram 1984, pl. 5, p. 219). Mazon Creek area, Will County, Illinois, USA; Francis Creek Shale, Carbondale Formation (Westphalian C), Pennsylvanian.

*Other material.* Eight additional specimens housed in the collections of the Illinois State Museum (ISM.14833, 14842, 14845, 14846, 14849) and the Field Museum Chicago (PE.23237, 37957, 37976) were observed for comparison with *P. secretanae*. All are from the Mazon Creek Lagerstätte, Illinois, USA.

For complete synonymy list prior to 1984, see Schram (1984).



**TEXT-FIG. 7.** A–D, *Palaeocaris typus* Meek and Worthen, 1865, Westphalian C, Pennsylvanian, Mazon Creek area, Illinois, USA. A, ISM 14849b, complete specimen with long antennae in lateral view;  $\times 3$ . B, D, ISM 14833, dorsal view of the cephalon with basal part of antennae and dorsal view of tail fan, respectively; both  $\times 8$ . C, ISM 14846, lateral view of a complete specimen;  $\times 4$ . E–F, *Palaeocaris retractata* Meek and Worthen, 1865, Westphalian D, Pennsylvanian, Coseley, Worcestershire, UK. E, In 29012, holotype in lateral view;  $\times 3$ . F, In 29013, cephalon and four first thoracic segments in lateral view;  $\times 10$ . All latex casts except E–F.

*Diagnosis* (after Schram 1984, modified). *Palaeocaris* with head length *c.* 0.25 thorax length. A1 with protopod longer than the two first components of A2. A2 with scaphocerite (exopod) longer than the two first components of the endopod. Sixth thoracic segment modified (triangular in lateral view). Triangular telson with small curved spines.

*Remarks.* Our observations confirm that the only external differences between *Palaeocaris secretanae* and *Palaeocaris typus* are those noted by Schram (1984) and concern A1, A2 (Text-fig. 7B), the sixth thoracic segment (Text-figs 7A, C, 8A–B) and the telson (Text-fig. 7D). To us, the shape of the sixth thoracic segment is an important character because of its evident implications in the flexibility of the animal.

*Distribution.* Apart from the type locality, *Palaeocaris typus* occurs at the abandoned Chieftain Mine, 11.3 km south of Terre Haute, Lower Shelburn Formation, Pennsylvanian, Indiana, and the abandoned strip mine talus, Pennsylvanian, 2.9 km west of Windsor, Missouri (Schram 1984).

1994 *Palaeocaris retractata* Calman; Schram and Secrétan, p. 156, fig. 1C.

1997 *Palaeocaris retractata* Calman; Anderson *et al.*, p. 200, fig. 2E.

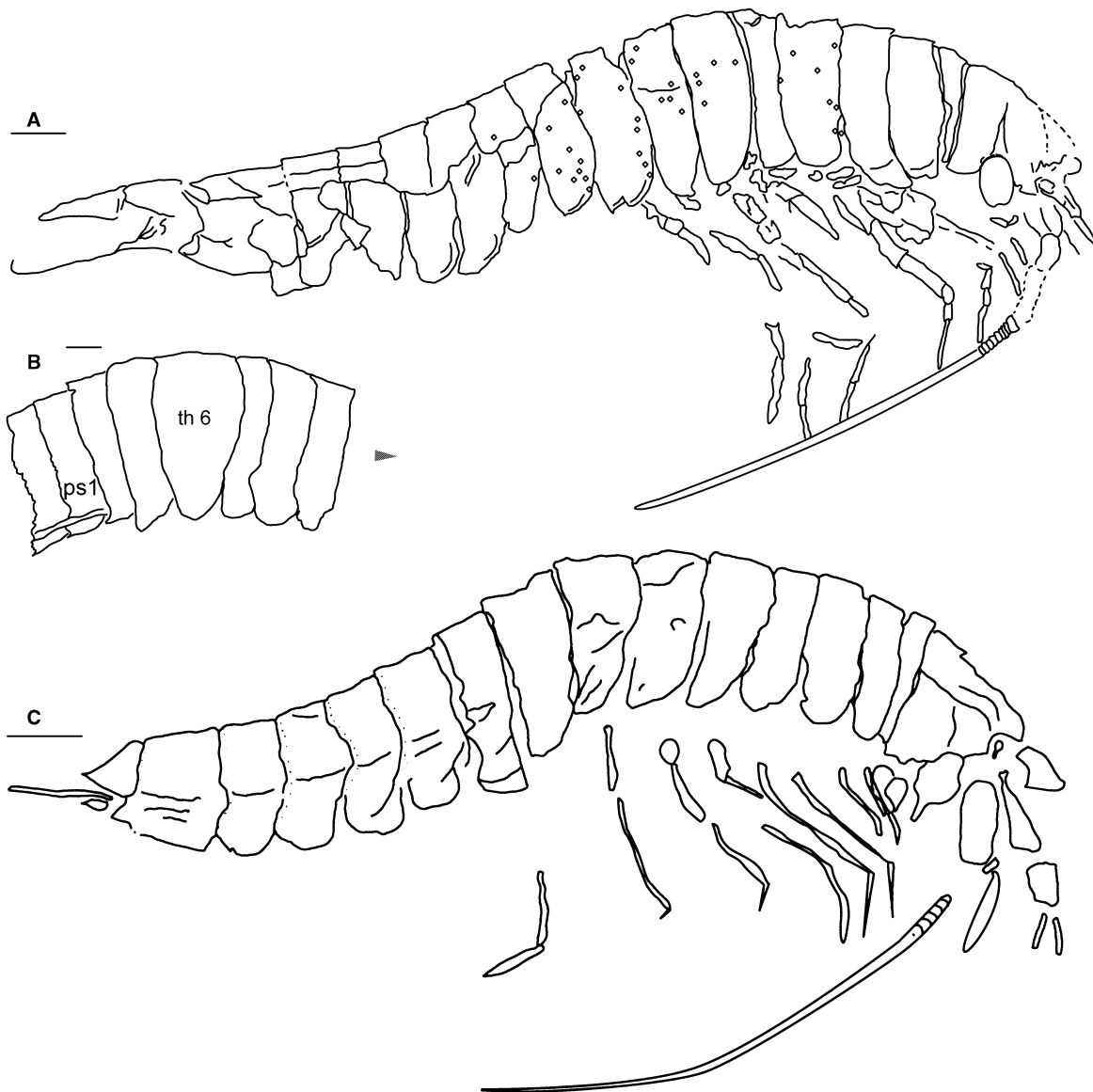
*Palaeocaris retractata* Calman, 1932

Text-figures 7E–F, 8C

1984 *Palaeocaris retractata* Calman; Schram, p. 219, pl. 5, fig. D; p. 220, fig. 16; p. 221, pl. 6, fig. A.

For complete synonymy list prior to 1984, see Schram (1984).

*Holotype.* Specimen In 29012, designated by Calman (1932), from Clay Craft open works, Coseley, near Dudley, Worcestershire, UK; Ten Foot Iron Stone, Lower Similis-Pulchra Zone, Middle Coal Measures.



**TEXT-FIG. 8.** A–B, *Palaeocaris typus* Meek and Worthen, 1865, Westphalian C, Pennsylvanian, Mazon Creek area, Illinois, USA. A, ISM 14849a (same as Text-fig. 7A), complete specimen in lateral view (small lozenges indicate pyrite crystals). B, ISM 14846 (same as Text-fig. 7C), sixth thoracic segment modified in lateral view. C, *Palaeocaris retractata* Meek and Worthen, 1865, Westphalian D, Pennsylvanian, Coseley, Worcestershire, UK, In 29012 (same as Text-fig. 7E), complete specimen in lateral view. Small arrow indicates front part. Scale bars represent 1 mm. Abbreviations as indicated in text.

*Other material.* Twelve additional specimens housed in the collections of the Geological Survey Museum (GSM.26720, 26721) and the Natural History Museum (I.13971, 15912, In. 29012, 29013, 29014, 29017, 29024, 62047, 62048, 62049) were observed for comparison with *P. secretanae*. All are from Coseley, near Dudley, Worcestershire, UK.

*Diagnosis* (after Schram 1984, modified). *Palaeocaris* with head length *c.* 0.35 thorax length. A1 with protopod longer than the two first segments of A2. A2 with scaphocerite shorter than the two first segments of the endopod. All thoracic segments similar except for the first one, which is strongly reduced. Telson oval, fringed with small curved spines.

*Distribution.* Apart from the type locality *Palaeocaris retractata* occurs on the west flank of Bilberry Hill, Lickey Hills, southwest of Birmingham, Warwickshire; Keele Beds, Westphalian D, Pennsylvanian (Schram 1984); and Bickershaw, Lancashire, UK (Anderson *et al.* 1997).

**GENERAL DISCUSSION**

The differences between *P. secretanae*, *P. typus* and *P. retractata* are tenuous (Text-figs 8–10). The length of the cephalic shield is the main character used by Schram (1984) to distinguish *P. retractata* from the other species (head to thorax length ratio being *c.* 0.35 in *P. retractata* and 0.25 in *P. secretanae* and *P. typus*; see Schram 1984 and Perrier 2003). Apart from these small size differences, the overall morphology of the head shield remains virtually identical in the three species.

The detailed morphology of A1 and A2 (Text-fig. 10A–B) may offer more reliable criteria to define species. Clearly the protopod of A1 is more developed in *P. typus* and *P. retractata* (longer than the exopod of A2) than in *P. secretanae*. Concerning the mandible, that of *P. secret-*

*anae* seems to be more powerful than that of *P. typus* and *P. retractata*, but detailed observations of the appendage (palp, incisor and molar processes) did not reveal convincing differences between the three species.

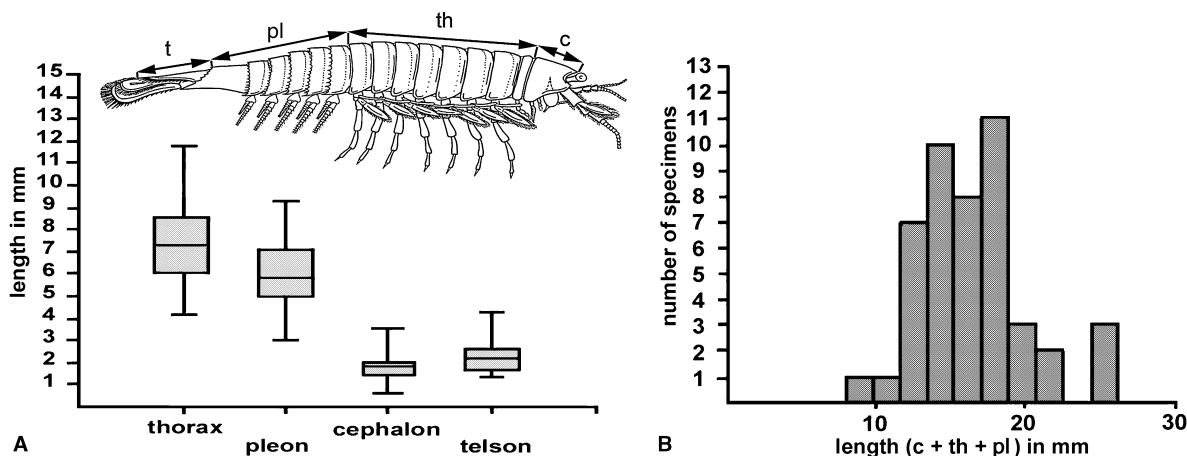
The morphology of the sixth thoracic segment is probably more useful. In *P. typus*, it has a most peculiar triangular shape (lateral view). Such a modification in the series of thoracic segments is unknown in the other two species and clearly has important implications on the articulation of the trunk as a whole. Perhaps *P. typus* had a more flexible trunk and a distinct locomotory behaviour.

Another key element that may provide more conclusive criteria is the telson (Text-fig. 10C). In *P. secretanae*, this is lobate and uniformly broad and has conspicuous strong spines inserted along its margins. In *P. retractata*, it is less robust and has a regular oval outline; moreover its spines are shorter, weaker and curved. The telson of *P. typus* has a distinctive triangular shape and is fringed with small recurved spines.

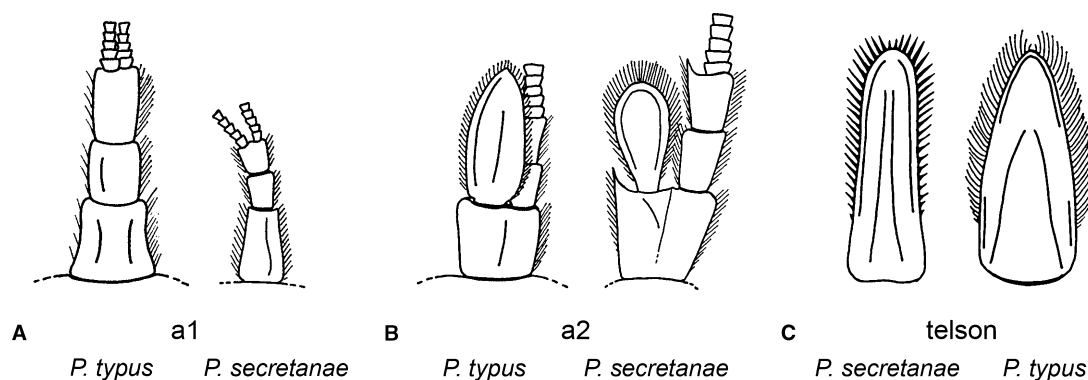
*Palaeocaris* displays an extremely narrow range of inter-specific variations. The lack of conclusive evidence for pronounced differences between *P. Typus*, *P. secretanae* and *P. retractata* strongly suggests very close phylogenetic relationships between taxa. Some of the differences, e.g. trunk articulation, telson and tail fan, and mandible size, may be interpreted as adaptive responses to specific requirements related to locomotion or feeding.

**TAPHONOMY**

The syncarids from Montceau are exceptional fossils for at least two reasons: the absence of major disarticulation of their body structure and the three-dimensional preservation of soft parts, e.g. eggs, and extremely fragile cuticular features such as appendages.



**TEXT-FIG. 9.** *Palaeocaris secretanae* Schram, 1984, measurements of 46 specimens. A, size distribution of the thorax (th), pleon (pl), cephalon (c) and telson (t). Boxes represent 75 per cent of the specimens. B, size distribution of c + th + pl as a whole.



**TEXT-FIG. 10.** Morphological differences between *Palaeoecaris secretanae* and *P. typus*. A, antennules (a1). B, antennae (a2). C, telson.

#### Lack of major disarticulation

Most syncarids are preserved as complete specimens. Sideritic nodules yielding only a fragment of the animal, e.g. isolated head or tail-fan, are extremely rare. Instead, it is the whole segmented body that is most frequently preserved, with its cephalic, thoracic and pleonal sections joined together. The presence of wrinkles between segments (Text-fig. 3A–B) indicates that the articulation membranes were not destroyed. On a smaller scale, numerous appendages are also complete, e.g. thoracic legs and appendages involved in feeding. Indeed, the fossil syncarids as they appear on the surface of split nodules show striking similarities to freshly killed syncarids of *Anaspides tasmaniae* preserved in alcohol (compare Text-fig. 3A–B with Pl. 1, fig. 1). The accurate lateral outline of the body (thorax + pleon), the spreading out of the tail fan and the way individual appendages are orientated (A2 flagella) or folded are virtually the same in both forms. This strongly suggests that the syncarids from Montceau have been fossilized in their life habit. Experimental studies on the decay of recent crustaceans greatly help us to understand the post-mortem history of the syncarids from Montceau and the environmental conditions that enabled their exceptional preservation. Several authors have noted that microbial activity had rapid and dramatic effects on crustacean carcasses left unburied in oxic conditions. Using *Neogonodactylus oerstedii* (Stomatopoda, Crustacea), Hof and Briggs (1997) observed three stages in morphological decay: swollen (due to osmotic uptake), ruptured (exoskeleton split) and partly decomposed (weakening of the cuticle, decay of soft tissues, disarticulation and fragmentation of exoskeleton). These experiments were conducted with artificial sea-water, sediment from a natural system (as a source of bacteria) and anaerobic conditions (vessels sealed in plasticized aluminium bag; method of Cragg *et al.* 1992). Hof and Briggs (1997) showed that the cephalothorax was

separated from the trunk after 4 days of decay and that most appendages were detached from the body after 25 weeks. Harding (1973) demonstrated that decay processes were amplified when temperature increased and that carcasses decomposed much less rapidly if buried immediately after death. Field experiments carried out by Plotnick (1986: intertidal localities) with *Pandalus danae* (Pleocyemata, Caridacea) showed that carcasses buried under 5–10 cm of sediment were rapidly damaged by scavenging and bioturbation whereas their preservation was largely facilitated below 10 cm. He also noted that preservation was better in mud than in sand.

Allison (1988) showed that, under laboratory conditions, the carcass of *Palaeomon*, a shrimp comparable in size and morphology to *Palaeoecaris*, underwent no major changes within the days immediately following the death of the animal. If unburied, the carcass lost virtually all of its appendages after 1 week due to intense microbial activity, but when buried in sediment, a few remains of appendages may still be present after 6 weeks. The conditions (oxic–dysoxic) that prevail within the sediment play a crucial role in the preservation of crustaceans. Rapid burial associated with anoxic conditions within the sediment, e.g. more than 10 cm depth (Plotnick 1986), increases dramatically the chances of segmented bodies being preserved. By contrast, when high energy in the depositional environment combines with microbial activity, carcasses can be very rapidly disarticulated and scattered (Brett and Braid 1986; Brett and Speyer 1990). Allison (1988) also pointed out that decay (under anoxic conditions) is more rapid in marine than in freshwater conditions.

Decomposition in most syncarids from Montceau was minimal and not more advanced than stage 1 (swollen) or 2 (ruptured; exoskeleton split) as defined by Hof and Briggs (1997). Undoubtedly, the carcasses were protected from both mechanical and biochemical (bacteria) damage by their rapid burial, the anoxic conditions that prevailed



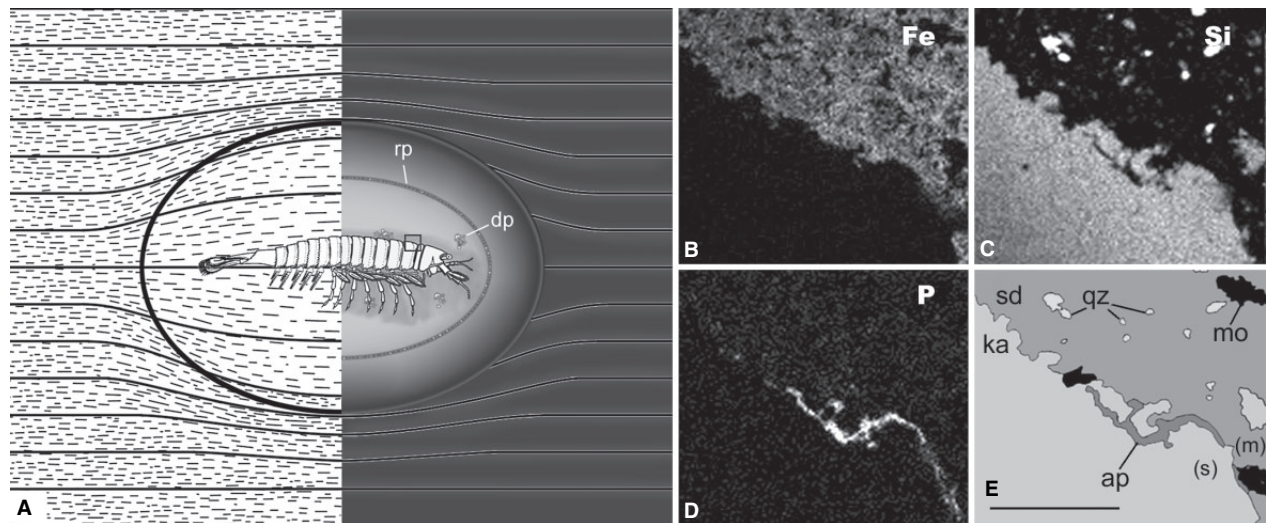
in the sediment and the lack of important disturbing agents, e.g. scavengers or bioturbators. Post-mortem transportation may have been minimal or absent. Fresh-water conditions may have hindered decay. The factors that caused their death are unknown. Oxygen depletion in the lower level of the water column may have killed the animals, which were then deposited gently within flocculent mud (no scavenging due to dysoxic conditions). More plausible though is the interpretation in which they were trapped by turbidity currents and buried in a few centimetres of mud. In this case, death and burial would have been almost simultaneous.

*Three-dimensional preservation*

Most syncarids from Montceau preserve the details of their original three-dimensional shape: for example, the head shield, the thoracic and pleonal segments (Text-figs 3A, D, Pl. 2, fig. 1), the thoracic appendages (endopods), the feeding apparatus (mandibles) and the lateral eyes. Although extremely fragile, the eggs have kept a perfect spherical shape. All these features show virtually no trace of collapse and flattening. Although cuticular elements may be relatively resistant to decay (Hof and Briggs 1997; see above), the rapid destruction of underlying soft tissues (epidermal cells, muscles, parenchyma) via microbial activity usually accelerates the collapse of body features. Early mineralization prevents collapse and allows

three-dimensional preservation. Numerous palaeontological and experimental studies have shown that phosphatization (apatite) is the most frequent of the mineralization processes (Briggs and Wilby 1996). The ostracod *Triadocypris* (Weitschat 1983; Vannier *et al.* in prep.) from the Triassic of Spitzbergen displays remarkably well-preserved anatomical details such as gills, appendages, muscles, eggs, lateral eyes with ommatidia and even ciliates attached to the surface of the cuticle. All these features are preserved in apatite. Similarly, microprobe-analysis (Text-fig. 11D–E) confirmed that phosphatization (presence of apatite) was responsible for the cuticular and soft-bodied three-dimensional preservation of syncarids. In our fossils, phosphatization is typically apparent as a black-reflecting thin layer. This led to the preservation of extremely fine structures such as sensory pores (diameter *c.* 5  $\mu\text{m}$ ).

Another factor played a key role in the preservation of syncarids. As with most faunal and floral elements of the Montceau biota, syncarids are preserved in sideritic nodules (Poplin and Heyler 1994). Precipitation of iron carbonate around the carcass (as the possible result of chemical changes induced by microbial activity) prevented syncarids from being rapidly flattened and strongly damaged by compaction. This hypothesis is supported by experimental taphonomy. For example, Hof and Briggs (1997) observed that water chemistry changed around dead crustaceans such as *Neogonodactylus oerstedii* (Stomatopoda). After only 3 days, the percentage of oxygen decreased from 50 to 3 per cent, and the pH from 8.00 to



**TEXT-FIG. 11.** Chemical composition of the fossil syncarid *Palaeocaris secretanae* Schram, 1984 from Montceau. A, schematic section through a sideritic nodule containing a syncarid. Tiny remains of vegetation (observed in lithological thin sections) underline very thin mud deposition within the nodule and the surrounding matrix; note that compaction is minimal within the nodule owing to early mineralization around syncarid carcass. Pyrite is present in the nodule, disseminated (dp) or forming a ring (rp). B–E, microprobe analysis of MNHN–SOT 3685a, element mapping of a section through second thoracic segment [(s) and (m) represent segment and nodule matrix]. B, Fe (sideritic matrix). C, Si (kaolinitic filling). D, P (mineralized cuticle). E, mineralization within the microprobe area: ap, apatite; ka, kaolinite; qz, quartz; mo, organic matter; sd, siderite; scale bar represents 50  $\mu\text{m}$ .

6:56, thus creating anoxic conditions around the carcass. Whether a nodule will form or not around a carcass largely depends on the iron concentration (Coleman 1985; Raiswell 1987). If iron is available in sufficient quantity, the conditions are optimal for siderite precipitation (Text-fig. 11B, E), especially in freshwater conditions (Berner *et al.* 1979; Walter and Burton 1990). It is the combined effect of siderite precipitation and phosphatization that probably explains the three-dimensional preservation of the Montceau syncarids and other associated fauna and flora.

#### Other minerals

Other minerals associated with syncarid remains were identified by microprobe analysis. The most frequent is kaolinite, which may fill up the inside of segments, appendages and eggs (MNHN-SOT 3685a, 74712a). Kaolinite is likely to have been produced by the alteration of the rocks surrounding the nodules (Text-fig. 11C, E). Calcite infillings were also frequently observed. Calcite seems to have crystallised preferentially in body cavities formerly occupied by soft tissues. Pyrite occurs either as a ring around the fossil (Text-figs 2A, 11A), as a thin layer on the surface of the cuticle, or in a disseminated form within the nodule (Text-fig. 11A). Chalcopyrite, baryte and celestine are also represented (Perrier 2003).

#### Conclusion

Although the taphonomic evolution and the chronology of mineralization are not completely understood, major steps leading to the preservation of syncarids have been recognized and may apply to the majority of fossils found in nodules as follows: (1) rapid burial in fine anoxic mud inhibited decomposition and disarticulation; (2) anoxia coupled with high iron concentration induced siderite precipitation, thus creating a protective microenvironment around the carcass (initial stage of nodule formation); (3) at the same time, phosphatization preserved cuticular and soft-bodied features (decaying organic material as a major source of phosphate); (4) other minerals, mainly calcite and pyrite, crystallized in cavities; (5) kaolinite filled up cavities and replaced former minerals.

## THE ANIMAL PALAEOCARIS

Key aspects of the palaeoautecology of *Palaeocaris secretanae* can be deduced from various lines of evidence, especially in regard to locomotion, feeding, sensing and reproduction.

#### Locomotion

The locomotion of syncarids was first studied by Manton (1930) (live observations of *Anaspides* and *Paranaspides*) and more recently by Hessler (1983) and Schram (1986) (live and laboratory observations of *Anaspides*, *Paranaspides*, *Allanaspides* and *Micraspides*). *Anaspides* and *Paranaspides* can crawl on the surface of gravel and aquatic plants using their eight pairs of thoracic, leg-like endopods. These consist of five, slender cylindrical segments, the most distal being the dactylus. They follow the basic design of malacostracan thoracic endopods (Mayrat and Saint Laurent 1996). The combined effect (often antagonistic) of four joints (each with apophyses + flexible articular membrane) allows the appendage to move in different directions (Manton 1977; Gruner 1996). Interstitial bathynellaceans do not crawl; instead they use their endopods to thread their way between sediment grains. *Palaeocaris secretanae* had thoracic endopods that are almost identical (although relatively finer) to those of *Anaspides* (Text-figs 4A, 12A–C; Pl. 1, figs 1, 8), which perhaps implies comparable locomotory mechanism. Two antagonistic articulations (at ischium-merus and merus-carpus boundaries, respectively) allowed the endopod of *Palaeocaris* to move parallel to the sagittal plane of the animal. However, the endopods are relatively small and fragile structures that may have only played a minor role in locomotion. The endopods are unlikely to have served in any powerful sense for crawling or digging. Instead they may have been used by the animal for anchoring or grasping, e.g. on sediment, plant fragments or detritus, or as tactile organs.

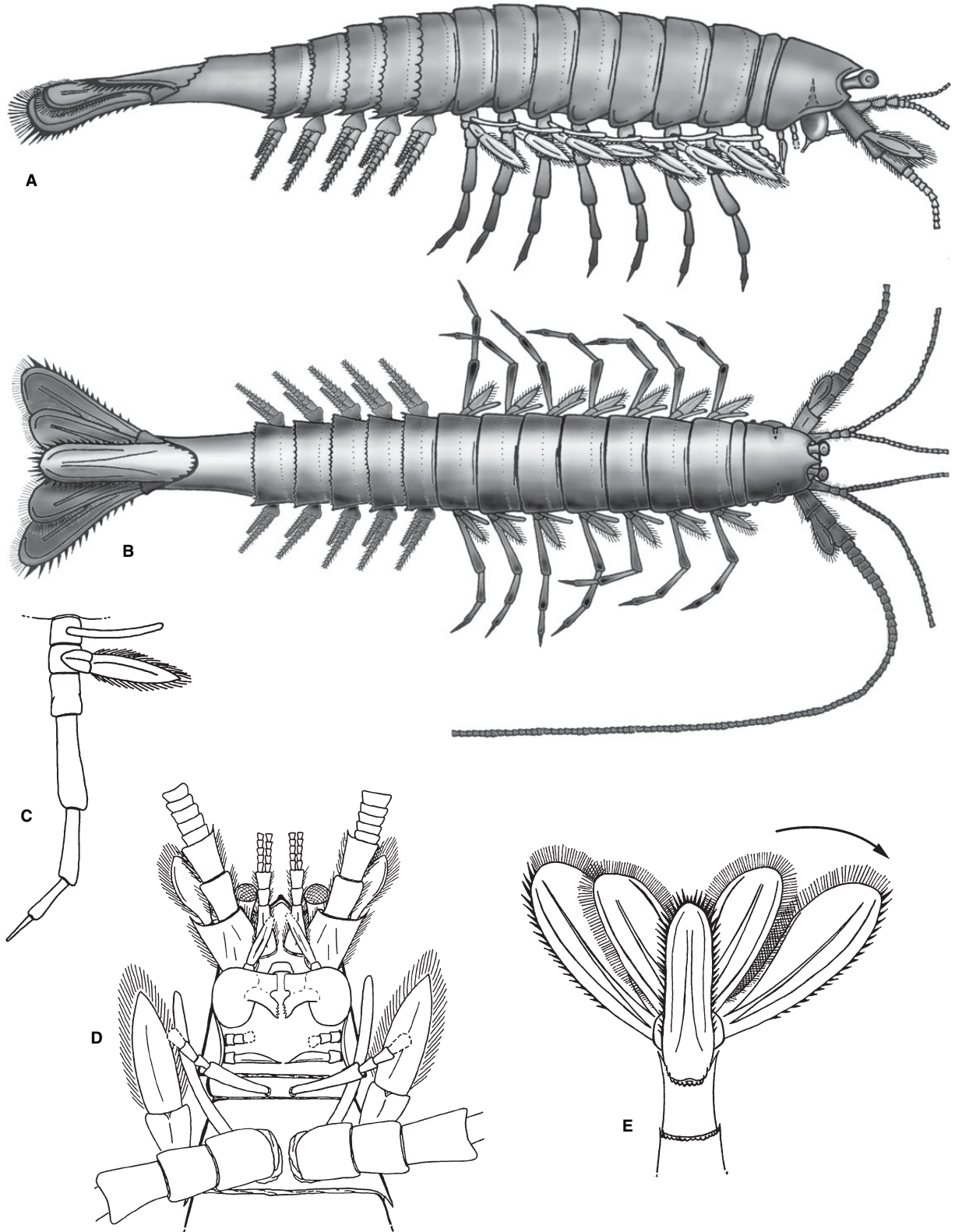
The anaspidaceans are, among present-day syncarids, the best swimmers. For example, *Paranaspides* swims by means of the combined action of its thoracopods and pleopods (Schram 1986). The exopods of *Anaspides* have a flattened lanceolate shaft and are constantly in motion in order to ventilate the epipods. This exopod is fringed

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**TEXT-FIG. 12.** Reconstruction of *Palaeocaris secretanae* Schram, 1984, Stephanian, Montceau-les-Mines, France, based on detailed observations of three-dimensionally preserved specimens and comparisons with present-day syncarids such as *Anaspides tasmaniae* from Australia. A–B, animal in assumed life position, lateral and dorsal views, respectively (long flagella of a1 and a2 not completely represented). C, thoracic appendage with leg-like endopod, scale-shaped exopod and cylindrical epipod. D, idealized ventral view showing feeding apparatus. E, tail fan in dorsal view; uropods are assumed to fan out (as indicated by arrow) in relation to locomotion (see explanation in text).

with setae that maximize resistance to the water when flexing backwards. Similar features are frequent in Recent crustaceans, e.g. phyllocarids (Vannier *et al.* 1997).

Although relatively small, the exopods of *Palaeocaris* seem to have had similar functions in both ventilation and swimming. Their orientation (MNHN-SOT 3996a)



suggests that they were able to swing strongly posteriorly (over 90 degrees with respect to the ventral body wall). Their backward, probably metachronal flexion resulted in the propulsion of the animal forwards. The exopods were also ventilating the ventral area of the animal. The epipods with an assumed respiratory function (exchange surface) are adjacent to the exopods (Text-fig. 4A–C). The pleopods of *Palaeocaris secretanae* are biramous (endopod shorter than exopod as in *Anaspides*; Pl. 1, figs 1, 9), multi-articulated, and bear numerous short setae (Text-fig. 4D). They were probably involved in locomotion like those of *Anaspides*, functioning in a metachronal manner, in tandem with the thoracopods to assist the animal in scuttling along the bottom.

The uropods of *Palaeocaris* are highly developed and create a large fan-like structure at the posterior end of the pleon (see Text-figs 4E, 12E; Pl. 2, figs 10–11) almost identical to that of *Anaspides* (Pl. 1). Their four-fold paddle shape reinforced by (1) closely spaced marginal setae (acting as an additional surface of resistance against water), and (2) strengthening features (along the axis and margins of the uropods) suggest an important function in relation to locomotion. For example, the downward flap of the caudal fan (triggered by powerful contractions of the pleon) would have generated lifting forces able to propel the animal obliquely upward in the water column. Other escape behaviours such the ‘caridoid escape reaction’ (quick contraction of the pleon muscles and backward escape using the uropodal paddle) are common among modern malacostracans, e.g. mysidaceans and euphausiaceans (Brusca and Brusca 1990) and performed by some syncarids such as *Paranaspides* (Schram 1986). Whether the pleonal articulation and musculature of *Palaeocaris* allowed the animal to use the caridoid reaction is not certain and cannot be deduced from our fossil specimens.

In summary, the absence of massive exopodal or pleopodal paddles indicates that *Palaeocaris* was not a very active swimmer in the water column. However, its highly developed caudal fan and high pleonal flexibility point to abilities to react quickly through an escape reaction to avoid predation. Swimming was probably accomplished close to the sediment-water interface. The very slender thoracic endopods were merely used for stirring up mud and supporting the animal rather than for crawling.

### Feeding

**Huge mandibles.** The most prominent cephalic appendage of *Palaeocaris secretanae* by far is the mandible. Its large size and swollen shape indicate that it was powered by strong muscles, as in Recent malacostracans with mandibles of comparable size. Important internal musculature is indirectly evidenced by the mandibular groove (attachment

area of muscles; Text-fig. 3C). The mandible of *Palaeocaris* has a palp, a processus incisivus and a processus molaris that are virtually identical to those of Recent syncarids such as *Anaspides* (see above; compare Pl. 1, figs 4–6 with Pl. 2, fig. 5; see also Text-fig. 12D). As in numerous malacostracans, the processus incisivus of syncarids is toothed and serves to tear small food items into pieces that are eventually passed to the processus molaris (grinding features such as stripes and tuberosity) (Gruner 1996). The palp often terminates with barbed setae and its function is to handle and maintain food close to the mouth (Coineau 1996). More generally in crustaceans, the position, orientation and the amplitude of movement of the mandible largely determine the feeding mechanism of the animal and have important implications for the size of food catch. For example, when the mandible axis is vertical, as in the anostracan *Chirocephalus diaphanus* (Manton, 1964), food is conveyed from the rear of the body to the mouth by the uniform series of thoracic appendages. This distinctive feeding mode only allows small particles to be ingested. By contrast, when the axis lies in a more horizontal position, such as in the isopod *Ligia oceanica* (Manton, 1964), the animal is able to catch larger pieces of food with its mandibles. In Recent anaspidaeans such as *Paranaspides lacustris* and *Anaspides tasmaniae*, the axis of the mandible is oblique (Watling 1983; Gruner 1996) allowing the ingestion of food particles of various sizes. Although fine details of the mandible of *Palaeocaris*, i.e. the palp tips and the ornament on processes, are not preserved, it is clear that its mandibular axis was oblique and that the mandible was probably functioning in the same way as that of Recent anaspidaeans, i.e. handling, grinding and ingesting relatively large food particles.

**Other feeding appendages.** The maxillule (Mx2) of *Palaeocaris* is flattened (Mx1 is poorly preserved). Its general morphology, position and orientation are similar to those of *Anaspides* and other malacostracans. Their most obvious function was to direct food particles towards the mouth and/or to sort sediment. The maxillae of *Anaspides* have numerous marginal setae used in capturing and filtering food. Such setae are not preserved or were absent in *Palaeocaris* (compare Pl. 1, fig. 4 with Pl. 2, fig. 5).

The posteriormost feeding appendage of *Palaeocaris* is the maxilliped. Again, it closely resembles the maxilliped of *Anaspides*, although it is relatively smaller. In malacostracans, the maxillipeds perform a variety of functions, such as assisting prey catch and maintaining food close to the mouth opening (Gruner 1996). The modest size of the maxillipeds of *Palaeocaris* excludes a significant role in predation. Instead, their main function may have been, along with Mx1 and Mx2, to direct food particles towards the mouth, and to groom the mouth parts (compare Pl. 1, fig. 7 with Text-fig. 3I).

*Palaeocaris* possessed a lobed labrum and a labium (although poorly preserved) that facilitated food intake.

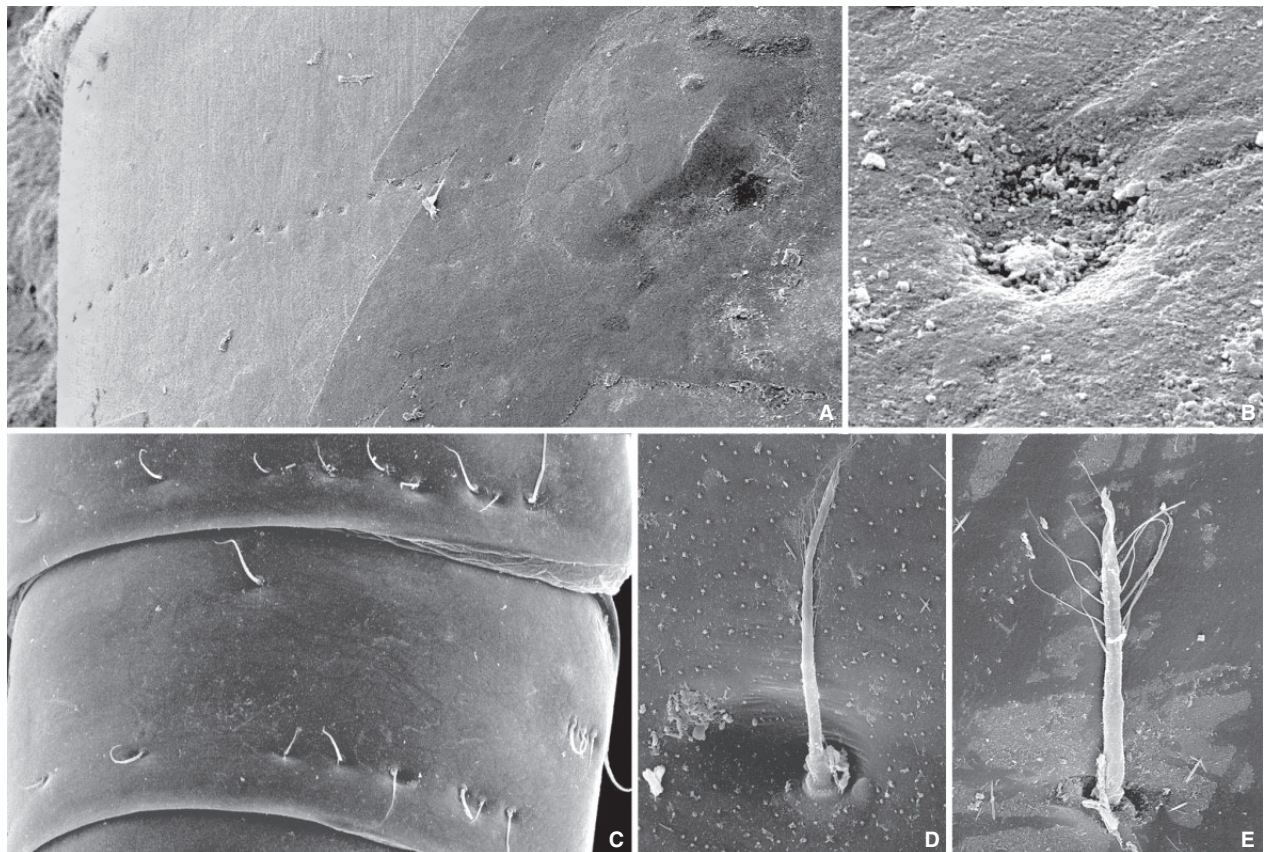
**Feeding mode.** The huge, obliquely inserted mandibles (with powerful associated musculature) of *Palaeocaris* strongly suggest an ability to catch and grind relatively large food items. The animal may have fed on a variety of detritus that was probably abundant at the water-sediment interface, such as plant debris, algae and decaying material. Predatorial habits are unlikely because *Palaeocaris* possessed no grasping appendages and had very small maxillipeds. However, predation upon poorly motile small invertebrates, e.g. worms, larvae and possible meiofaunal organisms, should not be excluded. The presence of mud within the gut of *Palaeocaris* may be a result of post-mortem filling but some sediment was probably ingested by the animal along with food. Studies on the feeding mechanisms and diet (gut contents) of Recent syncarids are rare. Predatorial behaviour is reported to occur in *Paranaspidetes* and *Anaspides*. For example, *Anaspides* is predominantly a detritus feeder, e.g. on animal or

vegetal remains as well as algal slime, but feeds occasionally on worms, tadpoles and insects (Coineau 1996; Wallis and Macmillan 1998). In *Anaspides tasmaniae*, when large prey is caught, the animal carries it around, grasped in its thoracic appendages, and consumes it extremely slowly, presumably in very small pieces (Wallis and Macmillan 1998).

*Allanaspidetes* is predominantly an omnivorous deposit feeder (Coineau 1996). By contrast, bathynellaceans obtain food, such as protozoans, fungi and bacterial films (Serban 1980), by scraping sand grains.

#### Sensory organs

**Vision.** Recent anaspidaeans such as *Anaspides* have compound eyes (Nilsson 1990) mounted on a peduncle (Pl. 1, figs 1–3), which increases eye mobility and provides the animal with a wide field of vision (Land 1996). By contrast, bathynellaceans have lost their eyes in relation to their interstitial lifestyle. The eye of *Palaeocaris*



**TEXT-FIG. 13.** Sensory pores of *Palaeocaris secretanae* Schram, 1984 (Stephanian, Montceau-les-Mines, France) and morphological analogues in Recent syncarids. A–B, MNHN-SOT 5795a, row of pores on a thoracic segment, general view and detail of a pore;  $\times 150$  and  $\times 2800$ , respectively. C–D, *Koonunga* sp. (Recent, Australia) showing sensory pores on successive thoracic segments (along posterdorsal margin), general view and detail of a pore with sensillum;  $\times 120$  and  $\times 900$ , respectively. E, *Anaspides tasmaniae* Thompson, 1894 (Recent, Australia), detail of sensillum;  $\times 1050$ . All scanning electron micrographs.

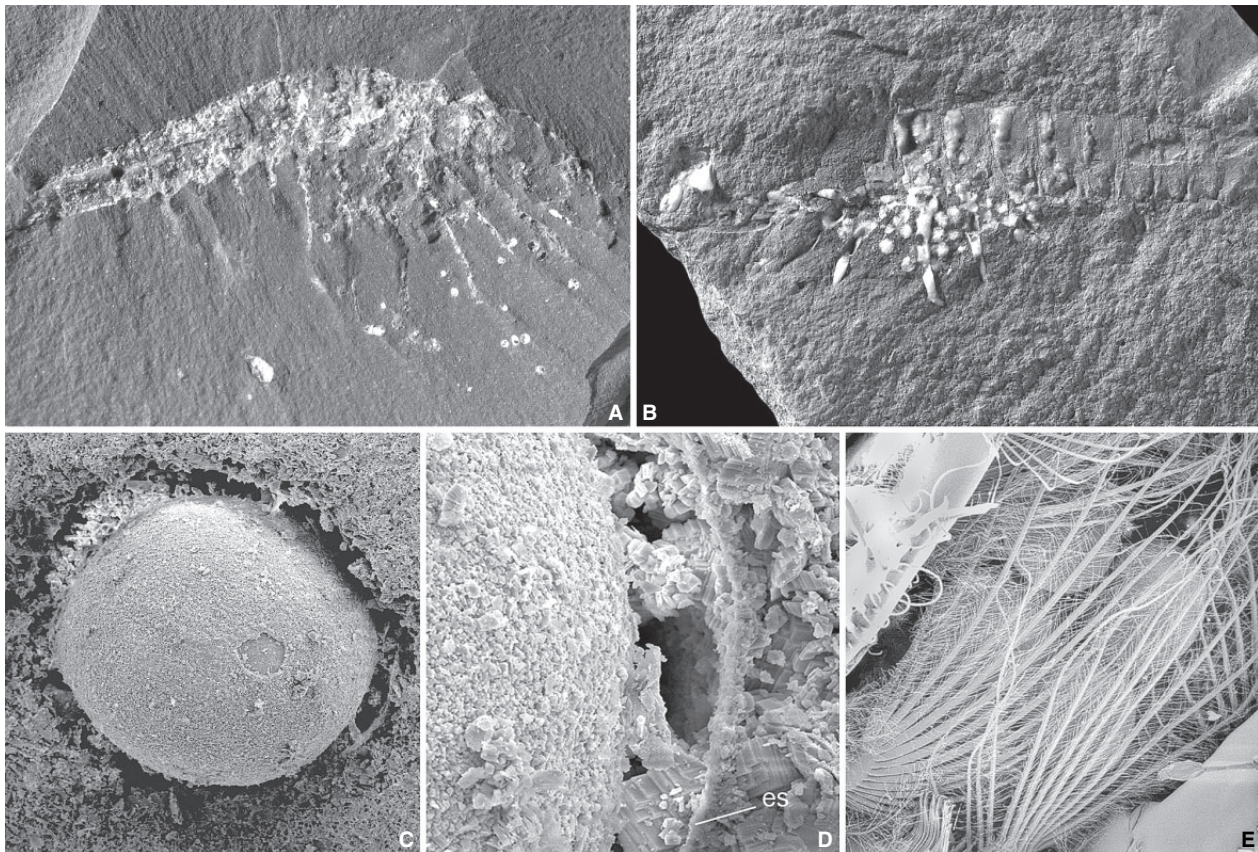
*secretanae* (Pl. 2, fig. 2; Text-fig. 3E–F) is stalked. The visual surface is covered by cuticle (ommatidia not visible). The eyes of *Palaeocaris secretanae* allowed wide frontal and lateral vision and were undoubtedly important organs used by the animal to locate food and to detect predators.

*Other sensory organs.* Similar to Recent anaspidaceans, *Palaeocaris secretanae* possessed an array of mechano- and chemo-receptors, as indicated by the presence of abundant setae on its frontal appendages (e.g. A1, A2; see Pl. 2, figs 3–4; Text-figs 5C–F, 10A–B). The trunk segments of *Palaeocaris* also possessed a sensory system made up of a series of rounded depressions, probably pores, evenly distributed along the frontal part of the second to thirteenth thoracic segments (Text-fig. 13A–B). Homologous features were found along the thoracic segments of *Anaspides tasmaniae* and *Koonunga* sp., each pore bearing a sensory seta (Text-fig. 13C–E). A tactile function is unlikely because of the dorsal location of the pores along the animal's body.

Perhaps, these sensory organs played a role in transmitting vibrations, thus bringing the animal information either on the velocity and direction of water currents or on the presence of other animals (Chaigneau 1996). These data would be particularly important for animals such as *Anaspides* that live in streams. A similar mechanosensory function is envisaged for the thoracic pores of *Palaeocaris*, although it is not clear whether the animal lived in streams or in more quiescent water bodies.

#### Reproduction

*Anaspides* and *Paranaspides* lay their eggs (diameter c. 2 mm) one by one under rocks or aquatic plants. *Anaspides tasmaniae* produces two different types of eggs: summer eggs, which develop over a period of 32–35 days, and winter eggs, which have a latent development (up to 60 weeks; Coineau 1996). The eggs of *Palaeocaris* (Text-fig. 14A–D) are 300  $\mu\text{m}$  in average size and typically



**TEXT-FIG. 14.** Brooding eggs of *Palaeocaris secretanae* Schram, 1984 (Stephanian, Montceau-les-Mines, France) compared with those of modern phyllocarids. A–B, MNHN–SOT 74685a and MNHN–SOT 5736a, two specimens with eggs between thoracic endopods or scattered in the vicinity of ventral appendages;  $\times 4$  and  $\times 6$ , respectively. C–D, MNHN–SOT 74685a, egg preserved in three dimensions, general view and detail of the assumed egg shell (es);  $\times 130$  and  $\times 680$ , respectively. E, ventral view of a recent female phyllocarid (*Nebalia bipes*, Roscoff, France) with brooded eggs maintained ventrally by long thoracic setae;  $\times 150$ . C–E are scanning electron micrographs.

occur as clusters along the ventral trunk. This might indicate that female (presumably) syncarids brooded their eggs. Recent phyllocarid crustaceans such as *Nebalia* keep their eggs against their ventral side by means of specialized, basket-like thoracic setae (Text-fig. 14E). Our fossils do not show such appendages. Instead, females may have secreted a sticky substance that could hold the eggs together. Perhaps the reproductive strategy of *Palaeocaris* was different from that of modern syncarids (anaspidaceans) owing to different environmental constraints.

## CONCLUSION

Taphonomic aspects show that the exceptional preservation of Montceau syncarids is due to (1) rapid burial, which protected the animal body from decay and scavengers, and (2) early diagenesis, with mineralization of the cuticle and the formation of a sideritic nodule around the animal. The detailed redescription of *Palaeocaris secretanae* Schram, 1984 and its comparison with *P. typus* Meek and Worthen, 1865 and *P. retractata* Meek and Worthen, 1865 suggest that these three species are very close morphologically. Apart from the thoracic dorsal articulation of *P. typus*, the differences within the genus only affect the size and shape of the antennae and the telson. The fine preservation of the fossil material allows accurate reconstructions of the anatomy of *P. secretanae* and reveals important aspects of the autecology of the animal, such as its locomotion (poor swimming ability, caridoïd escape reaction), feeding (probably omnivorous), vision (stalked eye, large and panoramic field of vision), sensing (rows of pores for current detection) and reproduction (brooding). In many aspects, *Palaeocaris secretanae* is very close to Recent syncarids such as *Anaspides tasmaniae* Thompson, 1894, which is found in freshwater streams in Australia. These morphological and autecological resemblances are probably due to a very similar life-style and environment.

*Acknowledgements.* We thank Cécile Poplin (Museum d'Histoire Naturelle, Paris) and Dominique Chabard (Musée d'Histoire Naturelle d'Autun) for access to the Sotty collections; Andrew Boulton (Armidale University, New South Wales) for Recent anaspidacean material; Frederick Schram (Amsterdam) for providing an updated list of fossil syncarids (Table 1); Jessica Theodor (Illinois State Museum, Springfield) and Charlene Fricker (Field Museum, Chicago) for the loan of specimens from Mazon Creek; Andrew Ross and Pauline Taylor (both The Natural History Museum, London) for the loan of specimens from Coseley (UK); Mark Williams (British Antarctic Survey, Cambridge, UK) and Nicole Coineau (Banyuls) for criticism and improvement of the manuscript; Noël Podevigne for photography and Philippe Grandjean for microprobe analysis (both Université Claude

Bernard Lyon 1). Vincent Perrier thanks Dominique Chabard, Daniel Sotty and the staff of the Musée d'Histoire Naturelle d'Autun for their hospitality during his visits (January 2002 and February 2003). This paper is a contribution to the Research Program of UMR 5125 PEPS (CNRS; UCB Lyon 1) on the 'structure and functioning of aquatic palaeoecosystems'.

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