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Devonian Eumalacostraca

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ABSTRACT

The archetype of the Eumalacostraca is believed to have had a carapace. With the description of a new crustacean fossil, *Eocaris oervigi*, n.g., n.sp., from the Middle Devonian of Western Germany, and reinterpretation of two fossils previously assigned to the Syncarida, phylogenetic theory is now supported by the fossil record. A new genus, *Devonocaris*, is established for *Palaeocaris cuylerensis* Wells from the Middle Devonian deposits of New York, and *Palaeocaris destinezi* Van Straelen from the Upper Devonian of Belgium.

Introduction

All theories for the phylogenetic origin of the Malacostraca accept the primitiveness of the Leptostraca. The paleontological record and studies in comparative morphology of Recent malacostracans support this interpretation. Therefore, the archetype of the Eumalacostraca must have had a carapace. It is perplexing that the most ancient authentic eumalacostracans reported in the literature are classified as syncarids and therefore supposedly lack a carapace. They are "*Palaeocaris destinezi*" Van Straelen (1943) from the Upper Devonian of Belgium, and "*Palaeocaris cuylerensis*" Wells (1957) from the Middle Devonian of New York.

Restudy of the alleged syncarids from the Devonian proves this taxonomic determination to be unsound. A new genus is required for the classification of these species, which are redescribed herein. A remarkable fossil with a carapace was recently discovered from the Middle Devonian deposits of Germany by Tor Ørvig of the Swedish Museum of Natural History. It is much better preserved than either of the above-mentioned fossils and represents a distinct new genus and species.

Animals without mineralized exoskeletal parts have left, at best, a sporadic fossil record of their evolutionary change through time. Though poorly preserved and incomplete, the Devonian eumalacostracan fossils are of great phylogenetic significance. They are the oldest fossils of this taxon known.

Descriptions of the fossils

The primary purpose of this paper is to describe the new Middle Devonian crustacean discovered by Dr. Ørvig. To do so requires redescription of the misinterpreted species, for which a new genus must be established.

Devonocaris, new genus

A single poorly preserved specimen from the Middle Devonian deposits of New York is of special interest in that it is the most ancient eumalacostracan from North Ame-

rica. The specimen was originally described as *Palaeocaris? cuylerensis* Wells. It is believed to be congeneric with the Upper Devonian species from Belgium named *Palaeocaris destinezi*. Not only are these species not *Palaeocaris*; they have none of the attributes of syncarids.

The telson of *Devonocaris* has no known parallel. It is spade-shaped. Though it is nearly rectangular, its margins are slightly convex. Its posterior extremity is nearly as wide as its base. A broad median ridge arises from the arched basal portion and extends the remaining length of the blade. The basal two-thirds of each lateral margin is reinforced by a rib.

All known morphological features of the type species, *Palaeocaris? cuylerensis* Wells (1957), are shown on the drawing (Fig. 2). They will be discussed below in the description. Etymology: Devon, Devonian; karis, a shrimp.

Devonocaris cuylerensis (Wells), 1957

Fig. 2.

Palaeocaris? cuylerensis Wells, 1957, p. 983–984, pl. 125, Figs. 1 to 4.

The description of the fossil and measurements were presented by Wells as the specific criteria for distinguishing this species. Morphological reinterpretation requires that new parameters be established. Measurements are as follows: length of body to the base of the telson, 16.8 mm; cephalothorax, 7.8 mm; abdomen, 9.0 mm; telson 2.7 mm; length of sixth thoracic somites, 0.6 mm; length of abdominal somites one to six, 1.5 mm; and the maximum width of the telson is 1 mm. The fossil appears to have been subjected to very little, if any, lateral spreading, thus it is worthy of note that the first abdominal somite is 2.5 mm and the last is 1.6 mm wide.

The fossil is preserved as a dorso-ventral compression of low relief in a black shale matrix. A carbonaceous residue of part of the exoskeleton remains. Some fine-grained pyritization has occurred.

Remains of the cephalothorax are fragmentary. Except for relics of the narrow tergites of the posterior thoracic somites, the dorsal elements of the exoskeleton were broken away in collecting. Remains of a carapace were undoubtedly destroyed. Vague traces of appendages can be seen. The long basal joints of the peduncle of both first antennae are present. The extremities of these appendages are too poorly preserved for interpretation. By holding the specimen at the proper angle relative to the light source, the right exopodal scale can be seen clearly. It is a narrow lobe fringed with setae. The other appendages are more evident when the specimen is wet with alcohol. However, the only statement that can be made is that the remains of the thoracic legs have a definite forward arrangement.

Six abdominal somites constitute slightly more than one-half of the body length. The first five are subequal in length and the last is somewhat longer. They narrow rapidly posteriorly.

Wells mistook the lateral portions of the blade of the telson for the endopods of the uropods. The uropods which arise from the sixth abdominal somite have a small sympod. The sclerotized outer margins of the exopods have left clear impressions. The membranous extremity and inner lobe are poorly defined. Vague suggestive remains indicate that both the exopod and endopod were lobate.

The body of the telson is the best preserved and the most diagnostic portion of the fossil. It is spade-shaped with a slight convex curvature of its lateral margins. The axial ridge that extends the length of the blade misled Wells into believing that the

lateral portions were the endopods of the caudal fan. He interpreted only the arched base upon which the intestinal filling terminates as the telson. Inward from the lateral margins are strengthening ridges. These diminish in height, but increase in width posteriorly. They originate near the basal margin of the telson and extend for three-fourths of its length. At their distal termination, the ridges have arched somewhat inwardly. Indeterminate remains posterior to the body of the telson are probably vestiges of the left furcal element and a median process. Both structures appear to have been small lobes.

SYNOPSIS

The cumalacostracan nature of the above-described remains cannot be doubted. Being from the Middle Devonian, this is the most ancient record of this taxon from North American strata.

Lack of a carapace on the fossil is negative evidence and proves nothing. The general appearance of the remains is of a caridoid crustacean. No syncarid is known with the thoracic endopods normally disposed in a forward arrangement. Also, the relatively large size of the telson and the relatively short length of the cephalothorax negates such a taxonomic assignment. It is believed that *Devonocaris* had a carapace.

The genus is characterized by the shape of its large telson. A definite specific characterization must await further discoveries.

STRATIGRAPHIC OCCURRENCE: Windon member of Moscow formation, 2 feet below base of Tully limestone, Hamilton group, Tioughniogan Stage (Givetian Stage of Europe), Middle Devonian.

LOCALITY: Quarry 1.5 miles northwest of Deruyter, Madison County, New York.

TYPE: Holotype, Cornell University No. 40020.

Devonocaris destinezi (Van Straelen), 1943

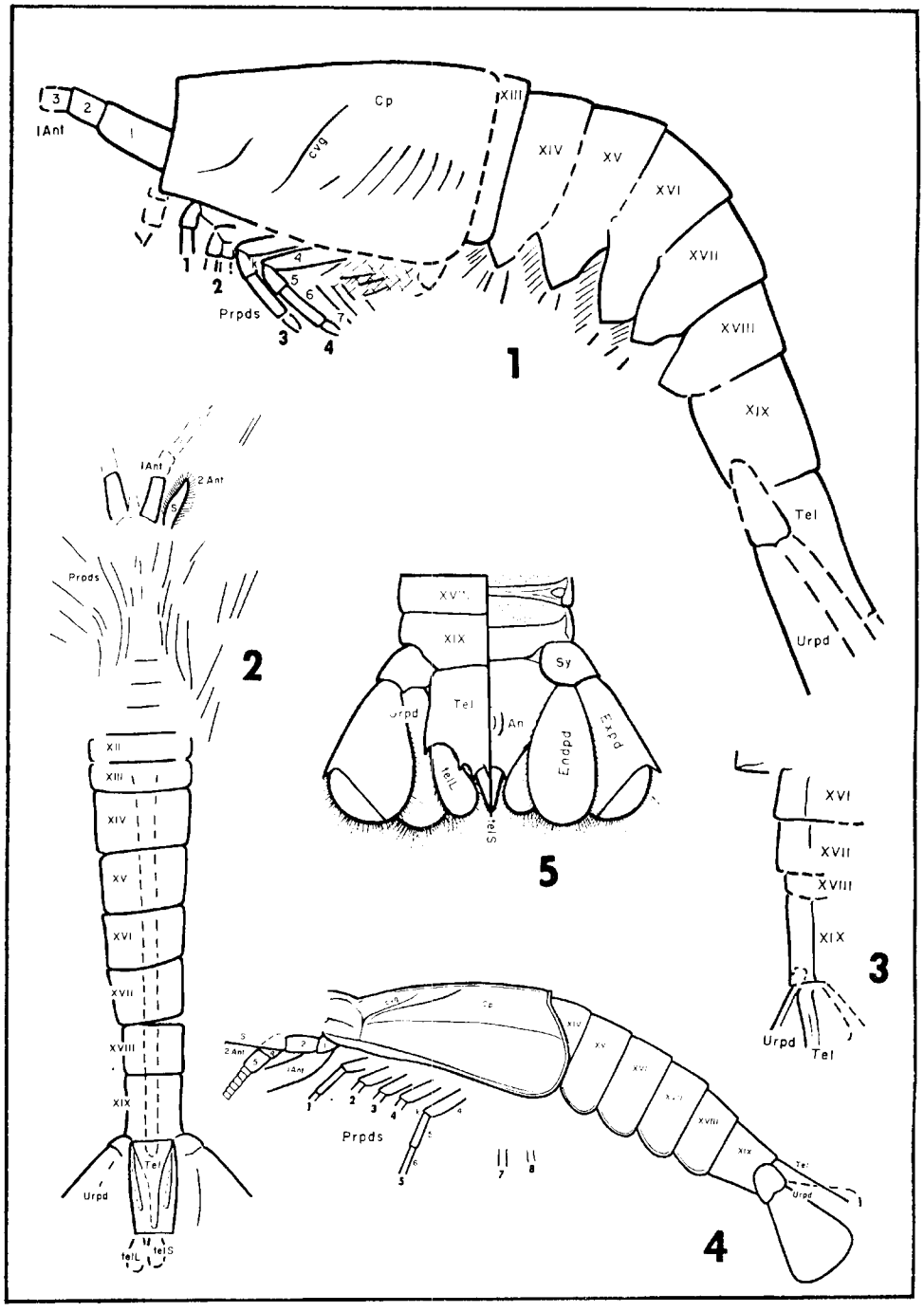
Fig. 3; pl. 1, Fig. 4.

Palaeocaris? *sp.* Destinez, 1907, p. 1366–1367.
Palaeocaris? *sp.* Destinez, Van Straelen, 1931, p. 16.
Palaeocaris destinezi Van Straelen, 1943, p. 1–5, 1 pl.

Only one fragmentary specimen of this crustacean has been discovered. It was first mentioned by Destinez (1907) as being related to *Palaeocaris typus* Meek and Worthen from the Upper Carboniferous of Illinois. It was later described as a new species and assigned to *Palaeocaris*. The reasons presented (Van Straelen, 1943, p. 3) were that the posterior border of the telson is round, the length of the uropods exceeds that of the telson, and the presence of a longitudinal carina on the exopodite of the uropods. Even if correctly determined, these characters are not unique to *Palaeocaris*.

The fossil is in a very poor state of preservation and it is understandable that differences of opinion should arise. It is believed the telson was spade-shaped and unusually long, and appears to have been very much like that of *D. cuylerensis*. Until better specimens are available, they must be classified together in the same genus.

The fossil is a dorsal impression of low relief of the posterior portion of the crustacean, the counterpart of which is missing. The matrix is an olive-drab, fine-grained subgraywacke. Fragments of marine invertebrate fossils, including an orthoconic cephalopod, are associated. Four tergites of the abdomen and portions of the elements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of the caudal fan are present as impressions. No residue of the original exoskeleton remains.

The total length of the relics is 30 mm. Therefore, it is estimated the total length of the animal was 60 to 80 mm. This is almost twice the size of the largest known species of *Palaeocaris*. The third abdominal tergite, which is the anterior element remaining, is 4 mm in length. The fourth and fifth tergites are overlapped. It is believed they were about the same size as the third. The tergite of the last somite is more than twice as long with a length of 9 mm. A prominent longitudinal median ridge is present on each of the tergites.

Except for the heavily sclerotized outer margin of the right exopod, the uropods are extremely vague on the fossil. An outline of a short joint believed to be the right sympod is impressed onto the tergite. The left lobate endopod can be distinguished with difficulty. As far as can be determined, neither ramus extended beyond the posterior extremity of the telson.

Only the right side of the telson is exposed on the fossil; the left is covered by matrix which separated at the level of the uropods. An arched median axis can be seen where some of the matrix has broken away. The telson is spade-shaped with its lateral sides slightly convex. Its posterior margin is transversely truncated. The length of the telson is 4 mm and its maximum width is estimated to be 2.5 mm. Its terminal breadth is slightly less than that of the base. On the blade of the telson lateral to the broad median ridge there is a subordinate longitudinal carina as on *D. cuylerensis*.

To the left of the fossil just anterior to the third abdominal tergite is an impression of a scrap of exoskeletal material which may be a portion of the second tergite. Nothing more can be determined about the fossil.

SYNOPSIS

Features that can be distinguished are not those of *Palaeocaris*, but of *Devonocaris*. The European species differs in the proportional size of the posterior tergite and the telson. The distal extremity of the telson is also narrower than the base. It is believed that the type species lacked the dorsal longitudinal ridge on each of the abdominal tergites.

STRATIGRAPHIC OCCURRENCE: Famennien Supérieur, Upper Devonian.

LOCALITY: "La Hesse", Tohogne, Luxembourg Province, Belgium.

HOLOTYPE: Laboratoire de Paléontologie Animale, Université de Liège, Belgium.

Fig. 1. *Eocaris oervigi*, new genus and species, Middle Devonian of Western Germany, ×5. Symbols used in the diagrams are: 1 Ant, first antenna; 2 Ant, second antenna; An, anus; Cp, carapace; cvg, cervical groove; Endpd, endopod; Expd, exopod; k, knee; Prpds, pereiopods; S, antennal scale; Sy, sympod; Tel, telson; telL, furca; telS, median articulated telson spine; Urpd, uropod; **1–8**, thoracic appendages; 1–7, joints of appendages, I–XIX, body somites.

Fig. 2. *Devonocaris cuylerensis* (Wells), Middle Devonian of New York, ×5.

Fig. 3. *Devonocaris destinezi* (Van Straelen), Upper Devonian of Belgium, ×1.5.

Fig. 4. *Palaeopalaemon newberryi* Whitfield, Upper Devonian of Ohio, ×2.

Fig. 5. *Anthrapalaemon gracilis* Meek and Worthen, Pennsylvanian of Illinois, restoration of dorsal and ventral features of the left side of the fifth and sixth abdominal somites and elements of the caudal fan, ×4.

Eocaris, new genus

It is unfortunate that the carapaces of the above-described species of *Devonocaris* are unknown. Whenever possible caridoid fossils have been defined by features of their cephalothoracic dorsal shields. The remarkable new specimen from the Middle Devonian of Germany is oriented on its side and thus superficially appears quite distinct. The only reliable distinguishing criterion is the reduced length of the thoracic tergites. Close relationship to *Palaeopalaemon newberryi* Whitfield (1880) from the very late Devonian of Ohio (Fig. 4) is suggested. The abnormally large size of the segments of the peduncle of the first antennae is a unique characteristic common to both. However, the shape and position of the transverse sulci on the carapace and the shape of the abdominal pleural lobes are not compatible with their assignment to the same genus.

Eocaris (Ety.: eo, dawn; karis, a shrimp) is an appropriate name for this, the most complete eumalacostracan yet discovered from the Middle Devonian. The type species, *E. oervigi*, is named in honor of its collector.

Eocaris oervigi, n. sp.

Fig. 1; pl. 1, Figs. 1–3.

The fossil is preserved as a flat lateral compression. Impressions of the compressed skeletal elements have extremely low relief. Fragmentary scraps of carbonaceous residue of the exoskeleton remain. The fossil is most obvious because of the lighter color of the sediment immediately adjacent to the crustacean. Though much of its morphology remains unknown, some significant features can be determined.

The shrimp-like fossil is of moderate size. The length of the body, less telson, is 42 mm. The carapace is 16 mm in length. Lengths of representative tergites are: eighth thoracic tergite 2 mm, fourth abdominal tergite 4.5 mm, and the length of the last abdominal somite is 6 mm. The telson is too poorly preserved for accurate determination of its length.

The cephalothorax is covered by a carapace. The eighth free thoracic tergite can be seen. From this, it is assumed that the carapace was not fused with the thorax. No rostrum is present and indications are that one did not originally exist. The anterior portion of the ventral edge of the carapace forms nearly a right angle with the straight anterior margin. No antero-lateral spine or other ornamentation appears to have existed. Two transverse grooves are present on the lateral portion of the carapace, but neither crosses the dorsum. The oblique posterior sulcus is equivalent to the cervical groove of other Eumalacostraca. The anterior groove is shorter and extends forward toward the antero-lateral angle of the carapace. In length, the cephalothorax is only two-fifths the length of the complete body.

Of the cephalic appendages, only the peduncle of the first antennae can be distinguished with certainty. The three joints of the peduncle extend forward. The basal joint is equal in length to the combined length of the other two. Both in length and diameter, these remains indicate an unusually massive base for the flagella. The flagella are unknown. Orbital space for the stalked compound eyes is present, but the eyes were not preserved. Extending from the antero-lateral corner of the carapace are scraps of an appendage. They may be two joints and fragments of the scale of one of the second antennae. The mandibles and two pairs of maxillae are unknown.

Being largely covered by the carapace, features of the thorax are difficult to determine. The eighth tergite extends beyond the carapace and is less than half the length

of the succeeding abdominal tergites. Seven oblique dorso-ventral lines impressed onto the carapace may represent sutures between the thoracic tergites. It is certain that the thoracic somites were greatly reduced in length. The sternites are unknown.

For the most part, the remains of the legs are a congeries of parts. A carpus and propodus of an endopod, probably of the first thoracic appendages, extends ventrally from near the anterior of the carapace. The next two appendages, one of which is superimposed, are believed to be the left and right endopods of the second pereiopods. Above these remains are two segmented elongate scraps. Close examination reveals that they are not vestiges of annulate flagella of exopods. The merus, carpus, propodus, and dactylus, with the "knee" between the merus and carpus, are well displayed by the third and fourth thoracic appendages (pl. 1, Fig. 2). Scraps posterior to these represent endopods, and possibly exopods and oostegites, but there is no decisive proof of this. In every case where Paleozoic caridoid Eumalacostraca are well preserved, the thoracic appendages are biramous. With few exceptions, e.g., *Anthrapalaemon gracilis* Meek and Worthen, the females also have a marsupium.

The first five abdominal tergites are subequal in length. In true shrimp-like fashion, the greatest flexure of the abdomen is between the second and third somites. These also have the greatest depth. The pleural lobes are unusually large for a Paleozoic crustacean. The antero-ventral edge is broadly curved. Posterior to the pointed apex, the margin of the pleura is straight for a short distance and then arches dorsally (pl. 1, Fig. 3).

Scraps below the abdomen no doubt represent vestiges of the pleopods. I cannot explain the parallel grooved membranous structure anterior to each pleural lobe (pl. 1, Fig. 3).

The last abdominal somite is about one and one-half times longer than the preceeding somites. Preservation of the posterior extremity of the exoskeleton is very bad. The sympod of the uropods is elongate. There are suggestions of two rami, but their existence cannot be verified with certainty. The telson was long, but its shape is unknown. There are dubious remains that may be articulated accessory structures at its posterior extremity.

SYNOPSIS

This shrimp-like eumalacostracan represents a distinct new genus and species. The genus, *Eocaris*, is distinguished from *Devonocaris* by the comparative shortness of the thoracic somites. It differs from *Palaeopalaemon* in the shape and position of the sulci on the carapace and by having large pointed pleurae on the abdominal tergites. It is believed that lack of ornamentation and the size and proportional development of the animal are specific characteristics.

STRATIGRAPHIC OCCURRENCE: Gray calcareous siltstone near the boundary between Givetian-Frasnian Stages, Middle Devonian. Associated fauna consists of phyllocarids (Jux, 1960) and fish remains (Ørvig, 1961).

LOCALITY: Large quarry at Eulenburg near Bergisch Gladbach, Rhenish Massif, Western Germany.

HOLOTYPE: Ar 47335, Dept. of Paleozoology of the Swedish Museum of Natural History, Stockholm, Sweden.

Phylogenetic relationships

Students of Recent Malacostraca all believe that the "caridoid facies" is primitive (Calman, 1909, p. 144, Glaessner, 1957). This hypothesis is undoubtedly correct and

with the corrections and evidence presented above is now supported by the paleontological record. *Amphipeltus paradoxus* Salter, 1863, Devonian; *Gitocrangon granulata* Richter, 1848, Devonian; *Necrogammarus salweyi* Woodward, 1871, Silurian; *Oxyuropoda ligioides* Carpenter and Swain, 1908, Devonian, and *Praearcturus gigas* Woodward, 1871, Devonian, have correctly been dismissed from serious consideration as the remains of Malacostraca (Van Straelen, 1931, p. 71–74).

Four authentic eumalacostracan fossils have been found in Devonian strata. They are *Devonocaris cuylerensis*, *D. destinezi*, *Eocaris oervigi* and *Palaeopalaemon newberryi*. Though these fossils are incompletely known, they are of considerable phylogenetic significance. All the eumalacostracan fossils from the Devonian and the Lower and Middle Mississippian (Lower Carboniferous) are now believed to have had a carapace. Though they display many adaptive trends, they belong to one genetic group.

No syncarid is known to be older than *Squillites spinosus* Scott (1938) from the Late Mississippian of Montana. Its original taxonomic assignment to the Stomatopoda is untenable. Calman (1932) demonstrated the species described as *Palaeocaris* by Peach (1908) to have short carapaces. A relationship with the Tanaidacea was suggested. This is also true of *Palaeocaris novascoticus* Copeland (1957) from the Mississippian of Canada. A separate paper is being published on syncarid fossils and their phylogeny (Brooks, 1962).

Several genera of Upper Paleozoic Eumalacostraca with a carapace are known which have a puzzling combination of morphological characteristics. All have biramous thoracic appendages and furcal lobes and a median articulated spine on the telson (Fig. 5). Adaptive structural trends toward the basic eumalacostracan types, i.e. peracarid, eucarid (decapod and euphausid) and hoplocarid, are displayed. These fossils have generally been called "pygocephalomorphs" from the first genus recognized, *Pygocephalus*, Huxley, 1857. *Tealliocaris* (Peach, 1908) from the Mississippian of Scotland has close affinities with the Mysidacea. On the other hand, *Anthrapalaemon gracilis* Meek and Worthen from the Pennsylvanian of Illinois lacks oostegites, has a seminal receptacle on the last thoracic sternite of females, and a secondary articulation between the mandible and the epistome has been established. These are characteristics of decapods! Two Mississippian forms, *Archaeocaris* Meek and *Perimecturus* Peach, are either remarkable homeomorphs of stomatopods or are archetypes. *Anthracophausia* Peach resembles the euphausids. The problems in classification are best exemplified by *Pygocephalus cooperi* Huxley, which not only has a peracarid marsupium, but the seminal receptacle diagnostic of syncarids and eucarids.

A vertical (phylogenetic) classification for these Paleozoic fossils consistent with taxa established for recent Eumalacostraca is impossible. Divergent evolution toward modern morphological types can be distinguished, but there is no proof that they are truly ancestral. Some may be the result of convergent or parallel evolution. All factors considered, a horizontal grouping is the only possible systematic solution. A monographic study of the morphology of the Paleozoic Eumalacostraca is nearing completion. In it the classification will be revised and new taxa established.

ACKNOWLEDGEMENTS

W. D. I. Rolfe of the Museum of Comparative Zoology, Harvard University, recognized the significance of a eumalacostracan in a collection of phyllocarid fossils from the Middle Devonian of Germany, made by Tor Ørvig of the Swedish Museum of Natural History. It is with their

cooperation and courtesy that the new fossil was studied. Prof. G. Ubaghs, Laboratoire de Paléontologie Animale, Université de Liège, and Dr. J. W. Wells, Department of Geology, Cornell University, graciously made the holotypes of the previously described species available.

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Uppsala 1962. Almqvist & Wiksells Boktryckeri AB

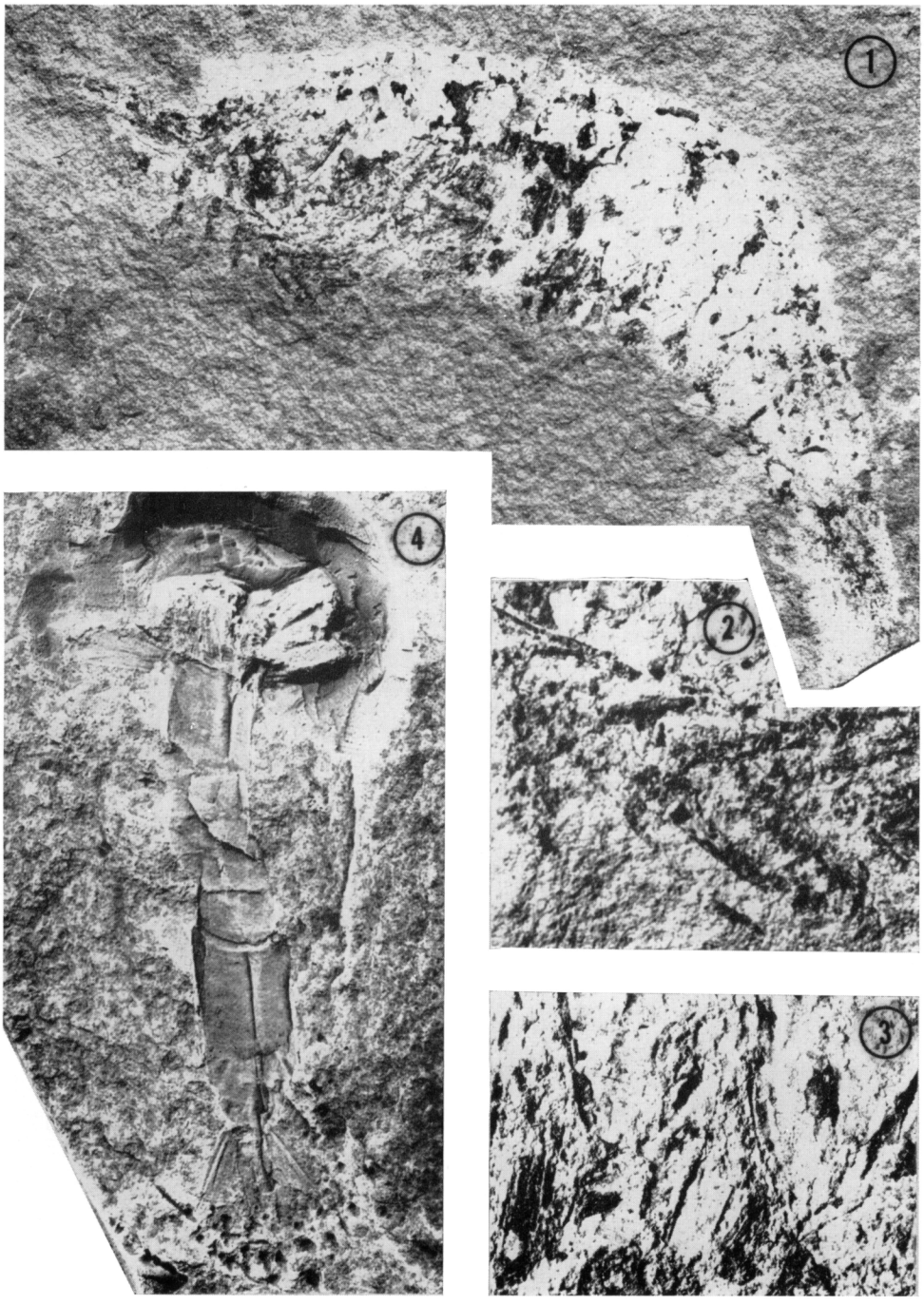
Plate I

Fig. 1. *Eocaris oervigi*, new genus and species, Givetian Stage, Middle Devonian, Rhenish Massif, Western Germany, holotype, × 5.

Fig. 2. Ibid., enlargement of pereiopods, × 10.

Fig. 3. Ibid., enlargement of third and fourth pleural lobes of abdominal tergites showing striated membranous structures, × 10.

Fig. 4. *Devonocaris destinezi* (Van Straelen), Famennien Stage, Upper Devonian, Luxembourg Province, Belgium, holotype, × 3.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