

Angustidontus, a Late Devonian pelagic predatory crustacean

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ABSTRACT: Restoration of the morphology of *Angustidontus seriatus* Cooper, 1936 based on complete specimens from the Famennian of Nevada and Poland, supports its affinity to the coeval alleged decapod *Palaepalaemon* and suggests eocarid (possibly also peracarid) affinities. Predatory adaptation of the thoracopods and the relatively short pereion make this crustacean only superficially resemble the archaeostomatopod hoplocarids, because the large grasping appendages of *Angustidontus* represent the first, rather than second, maxillipeds and acted in the opposite direction: downward. Another similar adaptation of the antennae in the Viséan *Palaemysis* suggests a widespread adaptation to predation among early eumalacostracans. The large sample collected from the Woodruff Formation of Nevada permits biometric characterisation of the grasping maxillipeds of *Angustidontus*, showing that their highly variable morphology should not be used to define species. All previously described species are therefore here synonymised with *A. seriatus*. Differences in gnathobases of mandibles found in articulated specimens in Nevada, and associated with isolated maxillipeds and articulated specimens possibly representing another unnamed species in Poland, suggest that such mandibles may eventually prove to be taxonomically more significant.

KEY WORDS: Eumalacostraca, evolution, Famennian, Hoplostraca, morphology, origin, Peracarida.

The main lineages of the eumalacostracan crustaceans were already differentiated in the Devonian but the fossil record of their early evolution remains highly incomplete. For some reason fossil eumalacostracans of that age are mostly restricted to pelagic rock facies: the most prolific Upper Devonian crustacean fossil assemblages are those from ammonoid-rich black shales. Well-sclerotised carapaces of the enigmatic crustacean *Concavicularis* aff. *bradleyi* (Meek) occur therein, commonly together with maxillipeds and pleons of the equally enigmatic *Angustidontus*. This association misled some authors to presume that these skeletal remains belonged to the same animal (Koch *et al.* 2003; Dzik 2005b) although complete specimens of *Angustidontus* were previously noted from the Famennian of Nevada (Rolfe & Beckett 1984). The cephalothoracic shield of *Angustidontus* is rarely preserved because of its weak sclerotisation, in contrast to the situation in the associated *Concavicularis*, where appendages are rarely preserved.

The toothed, comb-like appendages of *Angustidontus* were originally reported as fish jaws, but more recent comparisons have been made with eurypterid chelicerae, and with decapod or stomatopod appendages (Hannibal *et al.* 1990). Complete individuals described here show that these appendages are the greatly elongated first thoracopods modified for feeding (maxillipeds) of a eumalacostracan, perhaps showing some hoplocarid features. In the present paper the fossil material from the Famennian of Nevada and from roughly coeval strata of Poland is described, and a restoration of the whole animal is proposed, with discussion of its possible relationship to other Palaeozoic crustaceans.

1. History

Angustidontus and family Angustidontidae were established by Cooper (1936) for what he considered to be jaws of actinopterygian fish. Raasch (1956; Harker & Raasch 1958) suggested that these were the chelae of “*Pterygotus*, or some closely allied



eurypterid”, but Copeland & Bolton (1960) doubted this assignment. They compared them with gill rakers of fishes, or “raptorial claws similar to those on the second maxilliped of the stomatopod *Squilla*”, and noted a proximal “ball and socket” type of articulation for this appendage. Kjellesvig-Waering (1964) had seen “more nearly complete” specimens from Nevada which left him in no doubt that *Angustidontus* “was not of eurypterid nature. The specimens so far figured in the literature represent only the terminal part of the structures.”

Subsequent workers nevertheless tended to accept the eurypterid attribution, albeit with reservation (Jux & Krath 1974; Chlupáč 1978; Briggs 1979; Braddy & Dunlop 2000). A notable exception to this, as with so many fossil arthropod reattributions, was Leif Størmer. As early as 1966 (in Berdan 1983), Størmer agreed that these were not eurypterid, “but were of uncertain affinity, possibly decapod crustaceans.”

Over many years in the Paleontology and Stratigraphy Branch of the U.S. Geological Survey (USGS), the late Jean Berdan had had numerous *Angustidontus* appendages referred to her. She noticed a proximal article, together with the ‘ball and socket’ joint, and summarised information about the Nevadan material in a 1964 internal memorandum, subsequently (1983) enlarged and made available as an Open File Report. Her 1964 conclusion was cited by Smith & Ketner (1975, p. A31): “rami of *Angustidontus* are almost certainly part of an arthropod rather than a vertebrate but are not necessarily part of a eurypterid.” In 1981, Berdan drew this material to the attention of the senior author of the present paper and D. E. G. Briggs.

Intrigued by this material, and by Cooper’s (1936) observation that *Angustidontus* co-occurred with *Concavicularis* at several localities, and with little else save conodonts and anaptychi, W.D.I.R. undertook, with the help of Keith Ketner of the USGS, expeditions to the Nevadan locality in 1982 and 1983. The hope was that this locality would yield not only information about the appendages of *Concavicularis*, which it

did (Briggs & Rolfe 1983, p. 268, pl. 36, fig. 16), but might also reveal whether *Angustidontus* was another such *Concavicaris* appendage, which it proved not to be. Hundreds of specimens were collected, including the first complete animals, and these form the substance of the present paper. They show that *Angustidontus* belongs to a peracarid type of malacostracan, and that the association with *Concavicaris* was not as part of the same animal, but only as a separate element of a larger fauna, including fish, 'worms', cephalopods, bivalves, *Sphenothallus*, sponges, entomozoid ostracods and a discinid brachiopod. Preliminary results were presented at a 1984 meeting of the Royal Society of Edinburgh on the topic: "Fossil arthropods as living animals" (Rolfe & Beckett 1984).

Subsequently, Hannibal and Feldmann (1986; cf. Hannibal 1985) discovered a "toothed appendage", in new material of the supposed earliest decapod *Palaeopalaemon* from the Upper Devonian of Ohio. They suggested this was a raptorial "first pereopod" (actually perhaps the maxilliped?), not an antenna as had previously been thought, and later noted its similarity to the much less robust toothed appendage of *Angustidontus*, and to several of Ruedemann's (1935) supposed eurypterid chelicerae (Hannibal *et al.* 1990). Both taxa also have similar, characteristically short, hooked thoracopods behind the "toothed appendages". Abstracts only of this work have hitherto been available, and although a fuller account of what was to be a joint work was planned, and drafted by Hannibal and Feldmann, Rolfe's contribution was never completed.

With the discovery of new *Angustidontus* material in Poland (Dzik 2005b), again associated with a species of *Concavicaris*, it has become essential to publish what is currently known of *Angustidontus*, so that the Polish material can be set in context.

3. Occurrence and material studied

Angustidontus occurs, often abundantly, in the Upper Devonian to Mississippian of Oklahoma, Ohio, Indiana, Kentucky, Montana, Utah, Nevada, Alberta, British Columbia, Germany, the Czech Republic, and they are here reported from Poland. One report of the genus from the Silurian has been regarded as doubtful (Berdan 1983), while the Ordovician *Pseudoangustidontus duplospineus* van Roy & Tetlie, 2006 (van Roy & Tetlie 2006) is of uncertain affinity.

3.1. Nevada

Almost all material described here was collected from the headwaters of Woodruff Creek at Smith & Ketner's (1975, p. A29) locality 42, 43, which is shown on their map, pl. 1. This is within the type locality for the Woodruff Formation, in Carlin quadrangle, NE Nevada, and details of its stratigraphy, lithologies and biota are given by Smith & Ketner (1975). In a 20 October 1982 USGS "Report on referred fossils", based on material forwarded by Ketner and collected at this time, Mackenzie Gordon, Jr. reported on the ammonoids from this locality that they undoubtedly belong "in the *Platyclymenia* Zone (Famennian III B)", and that they closely resembled one from Ohio, subsequently described as *Pleuroclymenia ohioense* House, Gordon & Hlavin, 1986 (House *et al.* 1986).

More recently, the Woodruff Formation has been redefined to exclude rocks which, based on conodont determinations, included unrelated Lower Devonian and lower Middle Devonian strata (Sandberg *et al.* 2003). This does not affect the dating of the *Angustidontus*-bearing rocks, which still remain within the upper part of the now restricted Woodruff Formation.

The local succession in the Woodruff Formation was measured at locality 42, 43, where NW dips almost parallel the slope of the hill. The base of the succession here is a thick chert (unit A). It is followed up by 6–15 cm of cherty shale (unit B), 8 cm (unit C) and 13 cm of poorly fossiliferous silicified, shaly mudstone (unit D; C + D ranging up to 27 cm), 6 cm of very silicified shale (unit E), 15 cm (unit F) and 20–35 cm (unit G) of fossiliferous soft mudstone/shale in units 7–15 cm thick, c. 30 cm of thinly bedded shale, the lower 15 cm of it silicified (unit H), and terminates with 60 cm of siliceous splintery shale (unit I).

Material was collected by Keith and V. J. Ketner and the senior author in 1982 and 1983. Most of this material, 332 specimens, has been deposited in the National Museum of Natural History, Washington (NMNH) and allocated catalogue numbers of that institution. Detailed lists held by the Museum cite the lettering code applied on specimens and these indicate the collector, date of collection and the stratigraphic unit of the above succession from which it was obtained. Most of the 197 specimens of *Angustidontus* (and all articulated specimens) came from units G and, to a lesser extent, H. Specimens IR1 and IR2 were collected from different localities: IR1 came from 650 m N of locality 42, 43, from Carlin quadrangle NW1/4, NW1/4, section 30 (on line 25/30), T.32 N., R.53 E; IR2 came from Webb Creek, NE1/4, section 24, T.31 N, R52 E.

An additional 188 maxillipeds, which formed the basis of 1984 statistical analyses carried out at Glasgow University by E.C.M. Beckett, summarised here, have been deposited at the Hunterian Museum of the University of Glasgow, together with relevant paperwork.

Seventy-eight carapaces of *Concavicaris*, representing at least two species, have been recovered. The specimen USNM 393932 of *Concavicaris* aff. *bradleyi*, figured by Briggs & Rolfe 1983, p. 258, pl. 36, fig. 16, comes from this locality. 36 specimens of unidentified species of the phyllocarid *Sairocaris* (mostly isolated telson spines) have been collected.

The ammonoid *Pleuroclymenia* aff. *ohioense* is represented in the collection by a few crushed shells and anaptychi. Nautiloids are represented by several annulated and smooth longiconic conchs, and five fish scales and plates have been counted. The late S. Mahala Andrews earlier identified (*letter* 5 September 1984) a coelacanth in this collection.

The most common fossils associated with *Angustidontus seriatus* in the Woodruff Formation shale are the paper-thin shells of some species of the possibly epiplanktonic bivalve *Guerichia*; one specimen may represent an antipleurid bivalve. Also, the originally phosphatic flat tubes of *Sphenothallus*-type may represent epiplanktonic organisms. This is suggested by their preservation together with basal discs ('*Phosphannulus*'), sometimes in aggregations indicating the original attachment to an unpreserved, possibly organic, substrate. Rarely, also phosphatic shells of the discinid brachiopod *Schizobolus* occur, as do several 'worms' and sponges, together with entomozoid ostracods, probably one or more species of *Richterina* (*Richterina*).

The Woodruff Formation shale is secondarily decalcified and all the fossils are represented by moulds and empty cavities in the rock matrix. At least some of the carapaces were originally phosphatised, as shown by remains that survived weathering in some specimens. Usually remnants of carbonised cuticle are present but they are crumpled and exfoliate easily. A dark staining marks strongly flattened specimens and these were studied and photographed wet or covered with ethanol. Silicone and latex replicas were made of specimens with relatively strong relief.

3.2. Poland

Virtually all identifiable specimens of *Angustidontus* come from the abandoned quarry at Wietrznia (now within the limits of Kielce, the largest city in the Holy Cross Mountains area). There seems to be a single, 15 cm-thick, black calcareous shale bed yielding crustaceans, exposed in two places: in a rock left in the middle of the quarry and in the nearby wall to the east. Neither of these exposures shows the original stratigraphic succession and the fossiliferous shale forms part of large blocks within a tectonic breccia. Conodonts show the early Famennian age (*Palmatolepis crepida* Zone) of these strata (Dzik 2005a, 2006).

Compressed skeletal remains of *Angustidontus* and *Concavicularis* occur abundantly on bedding surfaces of the black calcareous shale in the middle of the 2.4 m-thick laminated marly limestone unit at Wietrznia. At this horizon arthropod cuticle is phosphatised and can be recovered by dissolving the surrounding limestone in formic or acetic acids. Numerous undeformed gnathobases of mandibles, maxillipeds of *Angustidontus*, and less fragile parts of carapaces of *Concavicularis* and telson spines of the phyllocarid *Sairocaris* have been obtained in this way from limestone beds occurring at these and several other localities in the area (Dzik 1980). The specimens embedded in laminated calcareous shale were cleaned with dilute formic acid. This increases contrast in coloration between the phosphatised cuticle and the rock matrix but only a little of the shale covering specimens can be removed in this way. They had first to be cleaned mechanically with a needle.

No other macrofossils are associated with the crustacean material, but in slightly more calcareous beds immediately below and above, an assemblage of fossils occurs, rather remotely similar to that of the Woodruff Formation. Instead of clymeniids, ammonoids are here represented by the goniatite *Tornoceras*. The most common fossils are isolated scales of placoderm fishes. *Schizobolus* is frequent. In limestone intercalations, smooth rhynchonelliform brachiopods, and articulated carapaces of the blind trilobite *Trimeroccephalus* can be found. There was an apparent change in composition of the crustacean fauna during the Famennian, mostly as a result of migrational faunal shifts rather than phyletic evolution *in situ* (Dzik 2006).

An unlabelled wooden box with fossiliferous marls, transferred to J.D. by Zofia Kielan-Jaworowska, was collected by her in the Holy Cross Mountains in 1946 for the late Jan Czarnocki. One of the calcareous shale slabs exposed an almost complete set of antennae and a series of pereopod appendages of *Angustidontus*. Conodonts extracted from a limestone concretion (sample Ko[?]-168 in Dzik 2006) indicate the latest *P. crepida* Zone of the early Famennian, which is consistent with the associated poorly preserved specimen of the goniatite *Cheiloceras* cf. *lagoviense* (Gürich) and the nautiloid *Gonatocyrtoceras* cf. *guerichi* (Sobolev). Strata of such lithology are now known only from the Kowala quarry and this seems to be the most likely provenance of this material.

All this material is housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (ZPAL).

4. Description

Unless otherwise indicated, this description and statistics are based on the Nevadan material, referred to above (see section 3.1). Statistics are cited thus: observed range (mean; standard deviation of the mean = \pm , with the number of observations = n).

Terminology follows that of the glossary in Moore (1969), with use of the term 'pleon' for the reasons advocated by

Waloszek & Müller (1997). We retain the term telson, even though this structure may actually be a pleotelson, since this remains the conventional usage for most Eumalacostraca, despite the long-known composite nature of that structure.

We have tried to be objective in our description of the often poorly preserved structures that we have observed in this material. At times, this may lead to description of incomplete morphologies different from those of extant eumalacostracans, e.g. only three podomeres have been seen comprising thoracopod 1, and only three or four podomeres in the hooked pereopods, whereas, by homology with extant taxa, their full complement was probably seven, as pointed out to us by Dieter Waloszek.

Furthermore, although we use the term maxilliped for the large toothed appendage that has hitherto proved so problematic, since we think this appendage is a homologue of the eumalacostracan first maxilliped, we have seen no evidence of the body segment on which this appendage articulated. We cannot know therefore whether such a segment was incorporated into the head, as is required for a strict definition of a maxilliped. Nor is there any evidence that this structure originated from any such appendage modified functionally into a maxilliped, and thereby much reduced in size. We employ the term maxilliped since morphologically, and apparently functionally, this unusual grasping appendage is situated first in the series of eight thoracopods.

4.1. Complete specimens

Eleven more or less complete specimens of *Angustidontus seriatus* have been collected. Two of these (NMNH 530438 and 530441; Figs 5a, 6a) are dorsoventrally flattened and lack appendages but the cephalothoracic shield is short in respect to the pleon, as in specimens bearing grasping maxillipeds diagnostic of *Angustidontus*. The cephalothoracic shield and the tail tend to be almost dorsoventrally compressed but oblique or laterally compressed pleons are equally common. This suggests that the shield and the pleon were almost as wide as high. The most complete specimen NMNH 530456 (Figs 1, 2b, c) is compressed somewhat obliquely.

Even when complete, specimens tend to be disarticulated and the shield is more or less displaced, which makes measurements unreliable. Proportions of the body parts can only be estimated but this suggests some allometry in growth. The shield length increased slower than the pleon length. Thus, in the smallest well preserved specimen (NMNH 530447; Fig. 4f) of 29 mm body length (without appendages), the shield represents about 39% of the total length; at length 34 mm (NMNH 530443; Fig. 4d) it is 37%; at 37 mm (NMNH 530457; Figs 3a, b, 4a, b) 38%; at 71 mm (NMNH 530456) 38%; at 74 mm (NMNH 530441 and 530435; Figs 5a, 6a, 3c, 4c) 34% and 29%, respectively.

4.2. Cephalothoracic shield

This structure is tenuous and presumably less sclerotised than the abdominal tergites and maxillipeds and, therefore, only rarely preserved. It is best preserved in the almost dorsoventrally flattened specimen NMNH 530456 (Figs 1, 2b, c), where a narrow rim demarcates its posterior margin, showing its transverse course at the dorsum and with gently rounded lateral lobes extending somewhat posteriorly. In specimen NMNH 530435 (Figs 3c, 4c) the shield is split medially in its anterior part and shows a medial ridge. In the laterally crushed smallest specimens NMNH 530447 (Fig. 4f) and NMNH 530434 (Fig. 4e) two mid-lateral carinae (or ?grooves as in hoplocarids) are present on each shield valve, subparallel to the dorsal midline. These shields are fragmented and it is

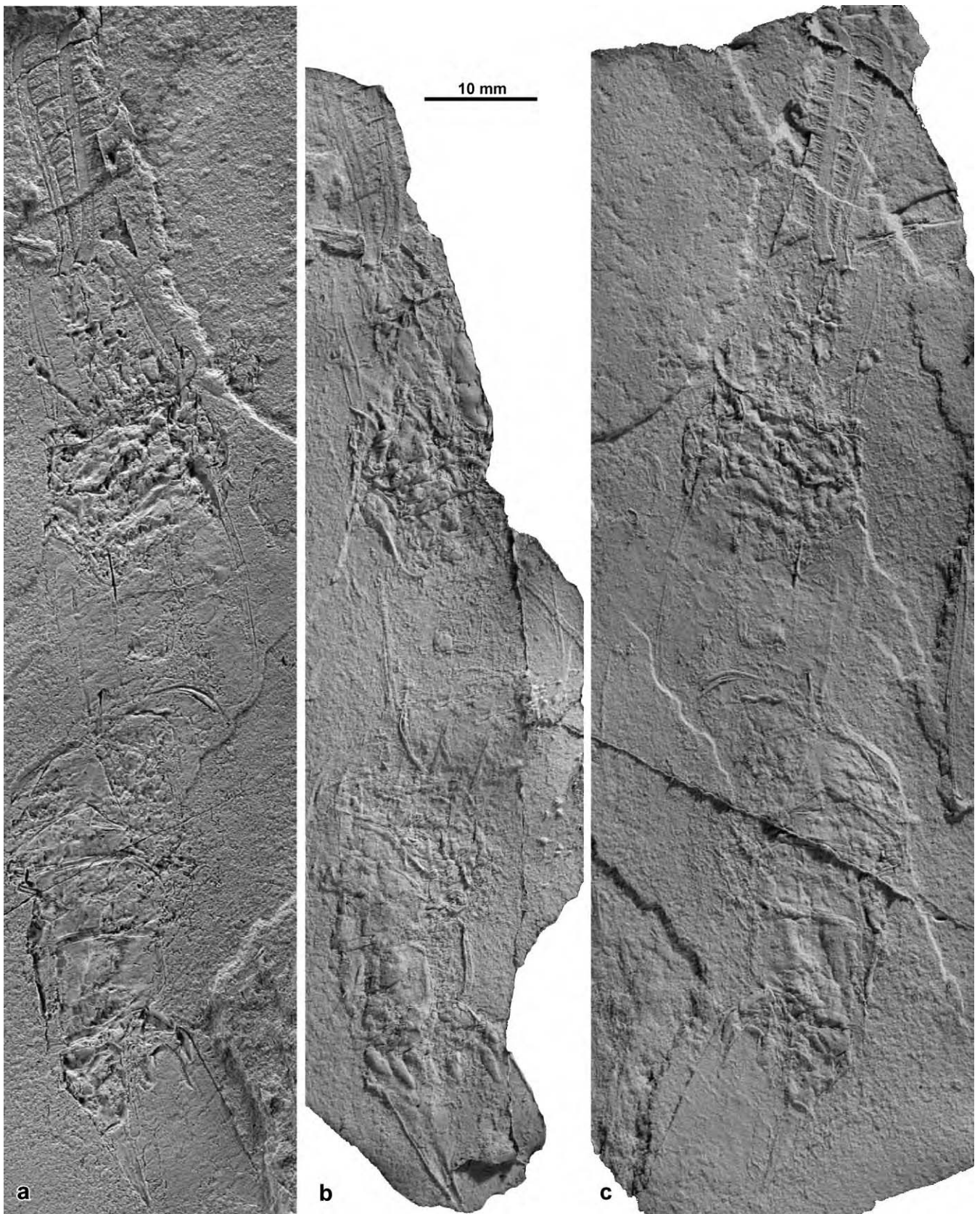


Figure 1 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada, *Platyclymenia* Stufe; most complete specimen NMNH 530456, see Figure 2b, c. (a) Part, whitened; (b) Latex replica of counterpart; (c) Latex replica of part.

difficult to determine the exact relationship between these structures. The anterior tip of the shield is partially preserved in NMNH 530456 and more completely in NMNH 530438: it

is gently rounded with a minute needle-like rostrum. Some minor lobation or denticulation of the margin seems to be present.

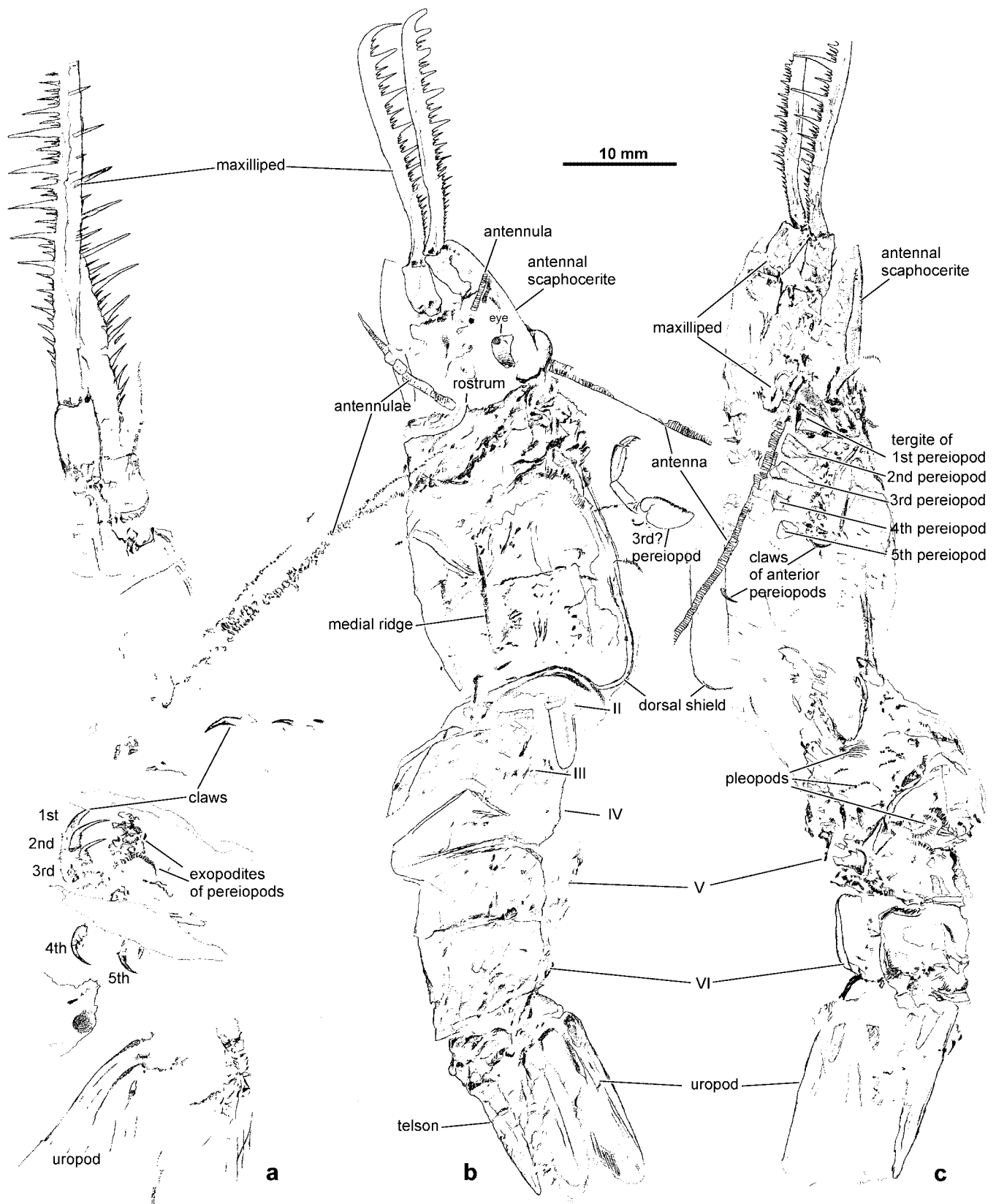


Figure 2 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; interpretative camera lucida drawings: (a) Largest complete specimen NMNH 530437; (b, c) NMNH 530456 part and counterpart, see Figure 1. Scale bar applies to all images.

4.3. Eyes

Pedunculate compound eyes are preserved well enough to be distinguished from the mass of crushed head cuticle only in two complete specimens. In NMNH 530457 (Figs 3a, b, 4a, b) they are represented by oval structures behind the bases of the

antennal scaphocerites on both sides of the specimen. In obliquely compressed specimen NMNH 530456 (Figs 1, 2b, c) the probable eye is club-shaped and displaced to one side of the head. Black regions near the end of the clubs probably represent corneae but individual ocelli are not discernible.

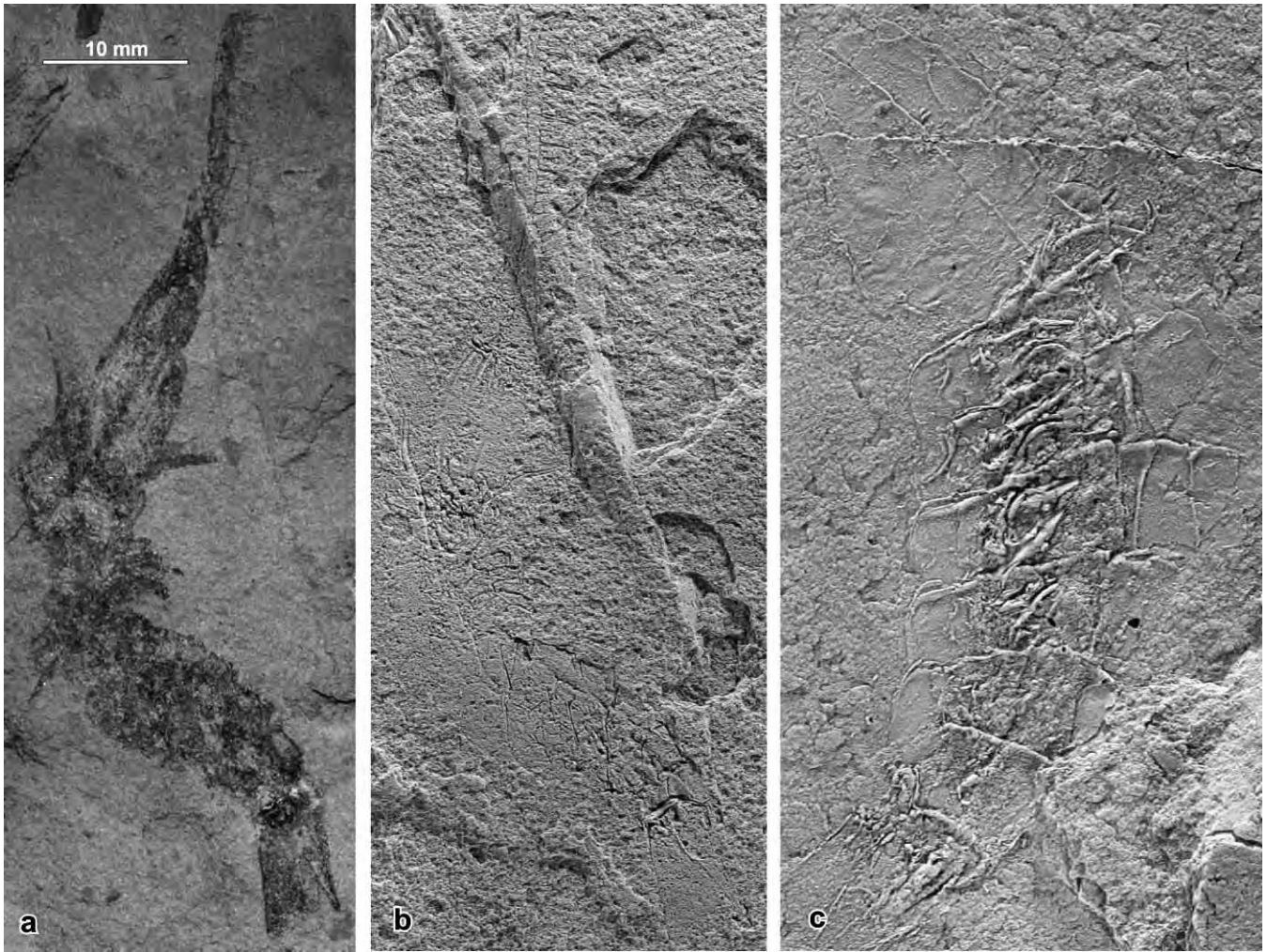


Figure 3 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; complete specimens: (a, b) NMNH 530457, part under alcohol and whitened, see Figure 4a, b; (c) NMNH 530435b showing sternites of the pleon, latex replica, see Figure 4c (reversed relative to this replica).

4.4. Sensory appendages

4.4.1. Antennulae. The biflagellate antennulae are about one third the length of, and slenderer than, the antennae. They are best represented in specimens NMNH 530436 (Figs 5b, 6b), NMNH 530458 (Figs 7b, 8a), NMNH 530448 (Figs 6h, 7a), and NMNH 530440. Each flagellum comprises more than seventy annuli, but details of the base of this appendage are not discernible.

4.4.2. Antennae. About three hundred annuli can be counted in antennal flagella of large specimens. The antennal exopod (scaphocerite) is carried on a short basal article (NMNH 530554) and has an almost straight outer edge. This is more robust than the inner edge, and a longitudinal ridge runs subparallel to the outer margin of the scale. The outer edge may be detached in the fossils from the more tenuous inner area, which passes laterally into a wide fringe of setae. Distally, the scaphocerite may bear one or two anteriorly directed spines, and it terminates in such a spine.

In NMNH 530451 (Figs 5d, 8e) a somewhat enigmatic structure resembling the scaphocerite is located in front of the mandibles. It bears a series of units resembling flagellar annuli along one of its margins. In NMNH 530450 the same kind of structure shows the probable annuli gradually decreasing in size towards the base of the probable scaphocerite. This can hardly be the flagellar base, because it is quite different from that visible in specimen NMNH 530448 (Figs 6h, 7a).

The attachment area of the antennal flagellum (endopod) is not well seen in any specimen. The basal, not annulated portion is represented in specimen NMNH 530448, but no details are discernible (Figs 6h, 7a).

4.5. Mouth appendages

In several cases, isolated aggregates of skeletal remnants occur, composed of mandibles and short mouth appendages armed with strong sharp bristles. The whole set of mouth appendages tends to stay together even after partial decay of the body, indicating some coherency of the ventral head cuticle.

4.5.1. Mandibles. These are usually preserved as internal and external moulds of the inner coxal edges only, found sometimes almost *in situ* in complete specimens (NMNH 530436; Figs 5b, 6b), but more usually isolated. The coxal gnathal lobe extends into a molar part with three or four low-crowned, ridge-like teeth (Fig. 10) set at right angles to the lobe. The incisor part is almost straight, ridge-like and forms about half of its length. A few strong teeth make its tip. The mandible body is *c.* twice the length of the gnathal lobe, wide and laterally rounded (Fig. 11o).

The mandibular palp is recognisable lateral to the incisor part of isolated mandible NMNH 530460 (Fig. 10a, b), but the palp attachment is not preserved and details of its morphology are obscured by crushing. A small transverse structure extending from the mandible body in its mid-length probably represents the dorsal muscle ligament (Fig. 10b).

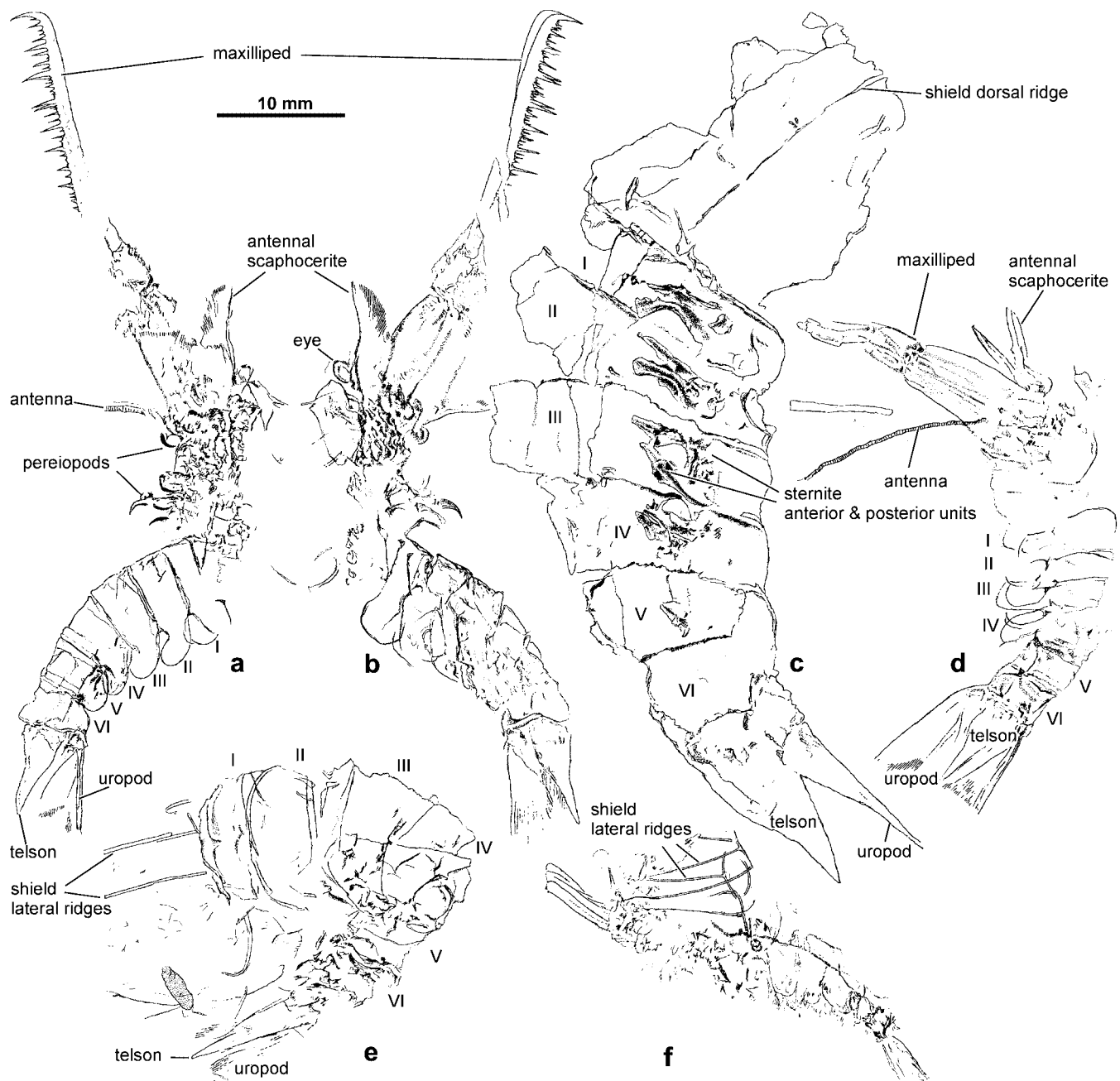


Figure 4 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; interpretative camera lucida drawings: (a, b) NMNH 530457, part, see Figure 3a, b, and counterpart; (c) NMNH 530435b, see Figure 3c; (d) NMNH 530443, see Figure 5f; (e) NMNH 530434; (f) NMNH 530447. Scale bar applies to all images.

Phosphatised three-dimensionally preserved mandibular gnathobases of the same morphology have been recovered from the upper Famennian strata at Jabłonna (J-24 and 28; upper *Palmatolepis trachytera* to *Pseudopolygnathus jugosus* Zones of Dzik 2006) in the Holy Cross Mountains, Poland (Figs 10e–h, 13d). No identifiable *Angustidontus* remnants have been recovered from these strata but the similarity of mandibles is so close that their identity seems likely.

In slightly older samples at Kowala and Miedzianka (*Platyclymenia annulata* horizon corresponding to lower *P. trachytera* Zone in Dzik 2006; Ko-8a and Md-18; Fig. 12a–q) somewhat similar phosphatised mandibles occur, but with only two transverse ridges of the elongate oval molar region and a strongly twisted incisor part (Fig. 12e, m).

Acid-resistant residues of limestone samples, collected at Wietrzna from the lower Famennian *Palmatolepis crepida* Zone strata (Wtr-21) immediately above the black laminated

shale with mass occurrence of crustaceans, yielded yet another morphology of the same kind of phosphatised mandibles. They have been recovered in association with fragmentary maxillipeds of *Angustidontus* (Fig. 14), and pieces of carapaces of *Concavicaris* with polygonal ornament. The mandible gnathobases from sample Wtr-21 have an almost circular molar part. The incisor part is neither linear nor zigzag-shaped, but composed of two transverse rows of denticles.

As is typical for malacostracan mandibles, the left and right gnathobases are not mirror images of each other (Fig. 12v, x) but transverse ribs on one mandible fit transverse depressions on the other. There is some population variability but all the identified specimens from this and other samples bear four slightly radiating teeth. Their size decreases posteriorly starting from the second tooth, which is slightly larger or of almost the same length as the anterior one. In the right mandible, all teeth are directed posteriorly and domination of the second tooth is

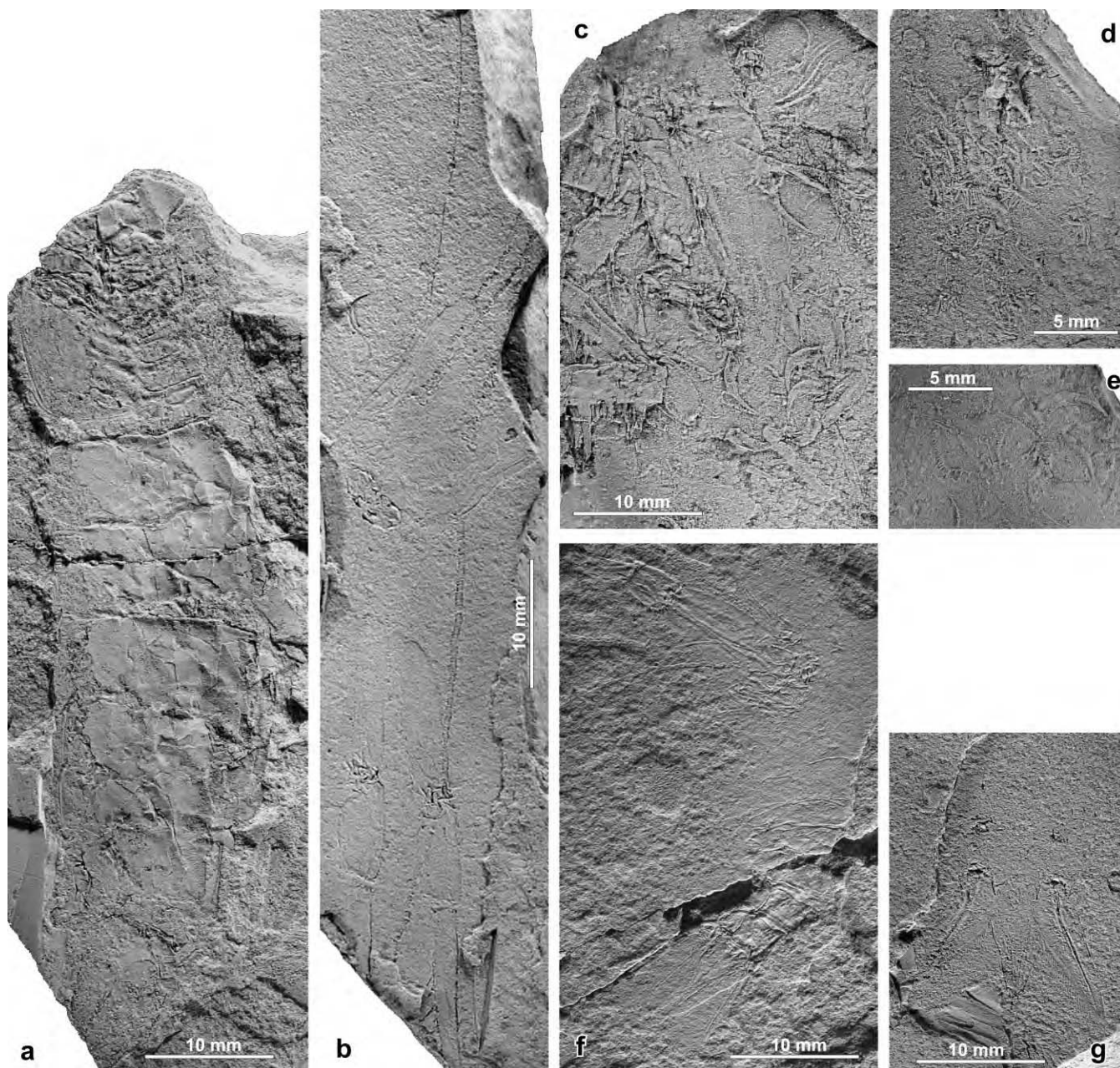


Figure 5 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; specimens whitened: (a) NMNH 530441b, see Figure 6a; (b) NMNH 530436, see Figure 6b; (c, d) NMNH 530451, latex replica of two associated specimens, see Figure 8d, e; (e) NMNH 530453b, latex replica of counterpart, see Figure 8c; (f) NMNH 530443, see Figure 4d; (g) NMNH 530445a, see Figure 9d.

more apparent (Fig. 12y). Both mandibles bear a structure corresponding in shape and location to a *lacinia mobilis* but which is not movable. It is trapezoidal in shape, with two weakly separated teeth and a ridge along its posterior margin. The molar part is subcircular in outline, with two transverse ridges composed of a few tubercles in the left mandible and a single transverse ridge in the middle of the right molar, its dorsal and ventral margins also forming ridges (Fig. 13b). The molars thus fit more or less in occlusion. Probably incisors and 'laciniae' of both mandibles interfingered while in action, but the material is too incomplete to determine precisely how they worked.

In some specimens under higher magnification, regularly distributed granulation is visible over the molar area, probably representing the bases of minute bristles (Fig. 12r).

Mandibles of this kind are widely distributed in early Famennian strata. For instance, they are represented in the Kuznetsk Basin of Siberia (lime plant on the Tomi River,

N.G. Izokh conodont samples B-8151–32/1 and E-9014–21/3, late *Palmatolepis triangularis* Zone), located on a separate continent in the Late Devonian.

4.5.2. Paragnaths. Immediately behind the mandibles a transverse row of strong spines can usually be discerned, even if their arrangement is somewhat chaotic. Well preserved mandibles are associated with paragnaths in specimen NMNH 530452 (Fig. 9c). Whenever they dip vertically into the rock, e.g. in specimens NMNH 530442 or NMNH 530449, it is clear that there is more than just a single row of spines along the margin. In the latter specimen a wavy membrane formed by unbranched filiform structures follows the mandible. These are either bundles of the mandibular muscles or bristles of the paragnaths.

The outline of paragnaths is visible in specimens NMNH 530450, 530452 (Figs 9c, 10c, d), and 530463. These are lobes of widths comparable with the incisor part of the mandible, with spines being largest near the external margin of the tip

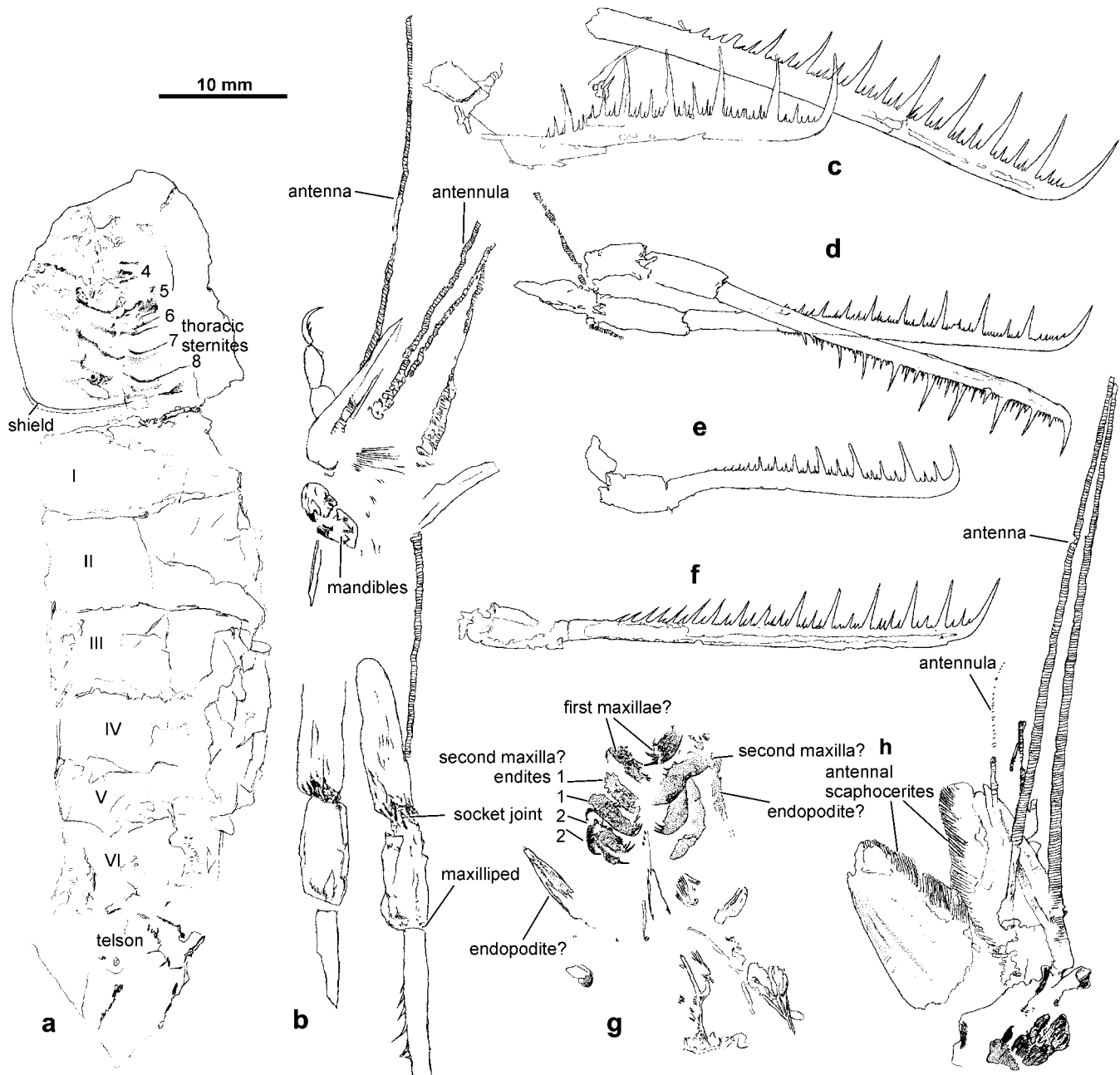


Figure 6 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; interpretative camera lucida drawings: (a) NMNH 530441b, see Figure 5a; (b) NMNH 530436, see Figure 5b; (c) NMNH 530454a; (d) NMNH 530453a, see Figure 7h; (e) NMNH 530461a, see Figure 7f; (f) NMNH 530455, see Figure 7g; (g) NMNH 530439a, see Figure 7d; (h) NMNH 530448a, see Figure 7a. Scale bar applies to all images.

and decreasing in size admedially. The external margin of the paragnaths is smooth.

4.5.3. Maxillae. A series of four tips of appendages, half the width of the paragnaths, occurs behind the latter. Each bears 4–6 denticles which seem to belong to the endites of maxillulae and maxillae. They are best discernible in specimen NMNH 530439, but even there it is hard to separate sets of the first and second maxilla (Figs 6g, 7d). Presumably, the two posteriormost spine-bearing lobes represent the basipodal endite, the two lobes in front of them may belong to the coxal endites of the first and second maxillae. From the base of this unit a poorly preserved structure emerges, which may represent the endopodite. The anteriormost unit, with somewhat stronger spines, seems to be the basipodal endite of the maxillula (=first maxilla).

4.6. Maxillipeds

The most significant feature of *Angustidontus* is the pair of large appendages which are slightly less than half the total body length, from the cephalothorax anterior to the tip of the telson (Figs 1, 2). Actual ratios of body length to total maxilliped length from the few measurable specimens are 1.25:1, 2.02:1, and 2.18:1. All that is known of this appendage are the three distal articles: any more proximal portions are unknown.

In a sample of 266 specimens from the Woodruff Formation, 179 comprise the distal toothed article only, 24 specimens show the two distal articles and 63 preserve three articles. The distal or third article of the appendage is slightly less than twice the length of the two more proximal articles combined, and ranges from 13.0 mm to 41.7 mm in length (mean 25.3 mm \pm 7.32 mm; n=78). The penultimate or second article

of the appendage ranges in length from 2.1 mm to 7.9 mm (mean 5.2 mm \pm 1.35 mm; $n=31$). The antepenultimate or first article of the appendage ranges in length from 1.0 mm to 16.9 mm (mean 9.03 mm \pm 3.46 mm; $n=30$). Of 286 specimens with the proximal end preserved, all but six specimens of the most distal article have a clearly defined, smooth toothless area adjacent to the joint with the penultimate article.

The proximal quarter of this article is often gently curved: 49 (38%) of 128 specimens show this feature (Figs 2b, c, 6e, 7f). In width, the whole appendage narrows distally, as shown by the following statistics: the width of the basal article ranges from 1.7–4.5 mm (mean 3.18 \pm 0.63 mm; $n=19$); second article 2.2–3.7 mm (mean 2.96 \pm 0.4 mm; $n=21$); third article 1–3 mm (mean 1.77 \pm 0.47 mm; $n=117$). The third article is usually the same width throughout its length, but occasionally it tapers distally.

The length of the toothed area of the distal article ranges from 8.2 mm to 34.3 mm (mean 21.84 mm \pm 6.1 mm; $n=78$). There is a high correlation between length of the toothed area and total length of this distal article (Fig. 15a).

Of 370 specimens collected, 47 comprise right and left members of a pair of maxillipeds. The teeth of these appendages are of six different, but discrete, lengths, with most specimens showing four tooth lengths, as shown on Figures 14, 15b. There is no statistical correlation between the number of tooth lengths and the length of the toothed area of the appendage. The possible significance of tooth length for species discrimination is discussed below (see section 5.1).

The proximal article was weakly sclerotised and is well preserved only in specimen NMNH 530436 (Figs 5b, 6b). Its base is gently rounded, which suggests oblique attachment to the body. There may also be a smaller basal protopodite, but this has not been securely observed (see Fig. 1c). The three articles articulate with one another by means of apparently paired condyles. These are prominent structures, which have been likened to ball-and-socket joints (Berdan 1983), but their preservation does not permit of detailed study and reconstruction. The second article is about one third shorter than the basal one, but of similar diameter and preservation. The distal toothed article is about 4.5 times longer than the second one and significantly narrower. It was originally flat and strongly sclerotised especially along its margins (Fig. 14). Teeth are usually missing near the base and the most proximal of them are small and strongly inclined.

The suggestion of direct attachment is supported by the laterally compressed specimen from Wietrznia, in which a kind of dorsoventrally extending tendon may occur at the base of the maxillipeds (Fig. 11o). Isolated grasping maxillipeds are the most common crustacean remnants on the bedding surfaces of the black calcareous shale at Wietrznia, but they are mostly fragmentary and crushed. Nevertheless, the most complete specimen ZPAL Cr 7/56c shows only three articles (Fig. 111, p, q), like the Nevadan form. The two basal articles were of oval contour and relatively lightly sclerotised. The distal article is usually aligned with, or at a slight angle to the basal article. It is unclear whether there was a true articulation at its base in the Holy Cross Mountains specimens or there was just a difference in the degree of sclerotisation. All specimens preserved well enough to show the pattern of denticulation are alike, with alternation in size of denticles of at least three orders. This is clearly visible also in chemically extracted appendage fragments (Fig. 14a, b). Especially resistant to fragmentation were terminal parts of the appendages with the last denticle series gradually increasing their size up to the appendage tip (Fig. 14c, d).

In dorsoventrally compressed specimens NMNH 530437 (Fig. 2a) and NMNH 530453 (Figs 6d, 7h) the appendages

have their teeth opposed to each other, which may suggest that they worked in occlusion. However, in NMNH 530457 and 530456 the teeth face in the same direction (Figs 1, 2b, c, 3a, b, 4a, b). Owing to their partial overlap in NMNH 530456 it is possible to determine their original orientation: they faced downward.

4.6.1. Tooth characteristics – shape, size, inclination. The teeth appear elongated-triangular in profile. Scanning electron micrographs of the German specimens illustrated by Jux and Krath (1974, fig. 12 a–4), as well as those from the Holy Cross Mountains (Fig. 14), indicate that the teeth were conical, with a robust wall. Their surface is finely longitudinally striated (Fig. 14e), mimicking associated conodont elements, despite the latter's order of magnitude smaller size.

Most teeth are straight, but the tips of some of the largest ones curve slightly in one direction; this curvature has been ignored for the purposes of the following statistics. The direction of tooth inclinations in the Nevadan material ($n=286$) is: distal 103; proximal 20; upright 119; indeterminate 44.

The length of the maximum tooth ranges from 1.0 mm to 6.8 mm (mean 3.5 mm \pm 1.5 mm). There is no statistical correlation between the length of the toothed area and the maximum tooth size.

Proximal teeth of the appendage are uniform in size and inclined distally, but proceeding distally their inclination decreases and the teeth become larger and variable in size. Direction of tooth slant features in previous descriptions of species, but several paired specimens occur with teeth sloping proximally on one and distally on the corresponding member of the pair. This distinction is therefore invalid as a specific character, although it may have resulted from compaction of the rock matrix.

Double teeth, i.e. two teeth of the same size beside each other, are present in a few specimens, although it is not clear whether this may be due to the presence of two specimens overlying each other.

In 196 specimens of this appendage, the total number of teeth ranges from 17 to more than 70. This probably represents ontogenetic development, but the teeth of insufficient specimens can be counted accurately enough to calculate statistics. The bimodal distribution in Figure 15c may reflect sexual dimorphism.

4.6.2. Diagenetic features. Many specimens show clear, circular areas from which cuticle is missing, along the length of the ramus of article 3 (Fig. 7h). These holes may fuse laterally to produce a bare, median, longitudinal strip (Fig. 7g). From the better preserved German material, this can be seen to be due to diagenetic replacement of the cuticle by a subsequently diagenetically destroyed mineral. The pattern was probably dictated by the original cuticular microstructure, perhaps similar to that established in the Silurian *Ceratiocaris papilio* Salter (Rolfe 1962).

A distinct groove, which often runs along the base of the teeth and separates them from the main ramus, may also be of diagenetic origin. It may in part reflect an ecdysial suture, since the appendage may be split apart along such lines.

4.7. Pereion

As noted above, the pereion is about a third to half the length of the pleon (NMNH 530441; Figs 5a, 6a). Although pereional segments can rarely be discerned, there are at least five of them; they are shorter than the pleonal segments. Their boundaries are marked ventrally by narrow, strongly sclerotised sternites.

In the most complete specimen NMNH 530456 (Figs 1, 2b, c) ventral tips of probable tergites are associated with pereion-pods. They are of rather uniform appearance and prove

separation of the pereional segments from the cephalothoracic shield. In Recent *Gnathophausia* species of size comparable with *A. seriatus* only the posteriormost tergites of the pereion are of similar appearance, with free tips; others are weakly sclerotised and their ventral margins merge linearly with each other.

4.7.1. Pereiopods. At least four pairs of distinctively clawed pereiopods are present (NMNH 530451, 530458, 530462; Fig. 8a, d), followed posteriorly by probably three further pairs of jointed appendages of more stenopodous form (NMNH 530459; Fig. 9a, b), which are probably pereiopods proper, i.e. locomotory thoracopods. A multiarticular flagellum in this position may be the exopod of one of these posterior pereiopods (Fig. 8a).

The enlarged basipod of the clawed anterior pereiopods is minutely toothed, forming a gnathobase. The terminal claw bears stout, claw-like spines on its inner surface, directed parallel to the tip of the main claw (NMNH 530464, 530440; Fig. 5c). All that can be discerned of each appendage are at least three articles of which the second is the longest (Fig. 2b). One specimen (NMNH 530465) shows four articles comprising the appendage, the extra one being a short article inserted between the basal and the second article.

A series of sclerotised hooks, apparently belonging to pereiopods, are recognisable also in at least three specimens from Wietrznia (Fig. 11). In specimen ZPAL Cr 7/4 from Kowala, a series of paired curved claws occurs parallel to the antennae (Fig. 11h, i). Either the antennae are oriented backward under the body or, more likely, they are displaced posteriorly together with the decomposed head and part of the body with mandible and pereiopods. If so, there would be a series of at least four pairs of claw-bearing post-maxillipedal appendages diminishing posteriorly in size. This agrees well with the data from the Nevadan form.

A flagellate exopod is preserved in some specimens (NMNH 530437, 530458; Figs 2a, 8a, b). These structures show indistinct annulation and bases of numerous setae.

4.8. Pleon

The six posteriorly tapering pleonal segments are of equal length, with rounded pleurotergal lobes (NMNH 530551). The posterodorsal border of these segments is spinose (NMNH 530444, 530466; Fig. 9f). In some specimens, a seemingly median spine may be produced by the margin of uropodal protopodites (Fig. 9d, f).

Well preserved pleonal sternites in NMNH 530435 (Figs 3c, 4c) show large openings for attachment of pleopods. A prominent node was developed in the middle of each sternite.

A rustily weathered concretion is occasionally seen in the last abdominal segment or telson area, and probably reflects the position of the anus (NMNH 530552). A similar feature has been described by Racheboeuf (1994) from the phyllocarid crustacean *Warneticaris cenomanense* Tromelin.

4.8.1. Pleopods. Pleopods are poorly preserved but apparent (NMNH 530444, 530553; Figs 2c, 4e, f).

4.9. Tail fan

This comprises a subtriangular elongate telson, flanked by setose uropods of similar length. The posterior half of the telson is straight-sided, whereas anteriorly the margins are wavy. Two longitudinal dorsal ribs on the telson converge posteriorly to form a single rib. Posterolaterally, the telson is shallowly notched, and stout setae can rarely be observed, seated in these notches (NMNH 530438). A maximum of nine such notches has been observed, and the number varies.

The uropodal exopod is large; it bears a longitudinal rib and a fringe of setae as broad as the exopodal blade but no

subdivision or diaresis is visible on specimens. Isolated exopods therefore resemble antennal exopods (scaphocerites), and can be difficult to distinguish from them. The inner edge of the uropodal exopod is convex proximally, concave distally (Fig. 9d). Uropodal endopods are rarely convincingly seen, largely concealed by the exopods, ranging from two-thirds the length of the exopod (Fig. 9e), to structures of the same length as the exopod (Fig. 2b). A feather-like appendage resembling the antennal scaphocerite, but with long setae on both sides of its distal part in NMNH 530452, seems to be a displaced uropod ramus (Fig. 9c). The protopods show pronounced articulation joints (Fig. 9d).

Some telsons appear tuberculate (NMNH 530438, 530466), but this may be due to the pattern of cuticle microstructure, or to adherent organisms.

The tail fan is well preserved also in the Wietrznia specimen ZPAL Cr 7/8 (Fig. 11n).

5. Taxonomy

5.1. Tooth patterns and species distinction

The type species of *Angustidontus* Cooper, 1936, *A. seriatus* Cooper, 1936, was diagnosed as having “teeth of five different lengths arranged in regular order”, whereas the teeth of *A. gracilis* Cooper, 1936 were of four lengths, only. Copeland & Bolton (1960) systematised this by assigning numbers to teeth of different lengths, 1 representing the longest tooth, 2 the next longest, and so on. Patterns characterising these species are as follows:

A. gracilis: 143424341 in repeating cycles

A. seriatus: 15453545254535451 in repeating cycles

A. weihmannae Copeland & Bolton 1960: 123414243414
234143413414142344 (pattern of holotype)

A. moravicus Chlupáč 1978: 1425341?3(?5)4(?5)4(?5)132(?5)
341543351(?5)32315234153231434(?)3241?342434 (pattern
of holotype).

On this basis (Fig. 15b), the Nevadan sample comprises largely the *A. gracilis* morphotype, with *A. seriatus* being only one quarter that frequent.

Previous workers have noted the variability of this tooth pattern character. Thus, in *A. weihmannae* “variation occurs especially on the anterior and posterior parts of the specimens” (Copeland & Bolton 1960, p. 37); while Chlupáč (1978, p. 237) noted in *A. moravicus* that the “relative size of denticles and their number within a cycle are variable in some degree and a strictly formal characterising [of] the species [*A. moravicus*] is not adequate.”

The relatively large samples of the Nevadan material also show highly variable tooth patterns. Many specimens possess patterns which are so unique that they cannot be matched with any previously recognised pattern, yet these unusual specimens do not form a pattern of their own. This suggests that the criterion of tooth pattern is not a valid one for distinguishing species. Furthermore, teeth which are broken, poorly preserved or buried in the matrix will prevent accurate assessment of this character. It is worth noting in this context that simply ‘removing’ the smallest size teeth from the *A. seriatus* pattern results in the *A. gracilis* pattern. Analysis of 171 assessable specimens from the Nevadan sample yields the following numbers of specimens referable to each of the previously proposed ‘species’: *A. gracilis* 86 specimens; *A. aff. gracilis* 29; *A. seriatus* 9; *A. weihmannae* 3; *A. moravicus* 1; different from foregoing species 43. So many sympatric species seems unlikely, and the following tests were devised to check the validity of the species referred to *Angustidontus*.

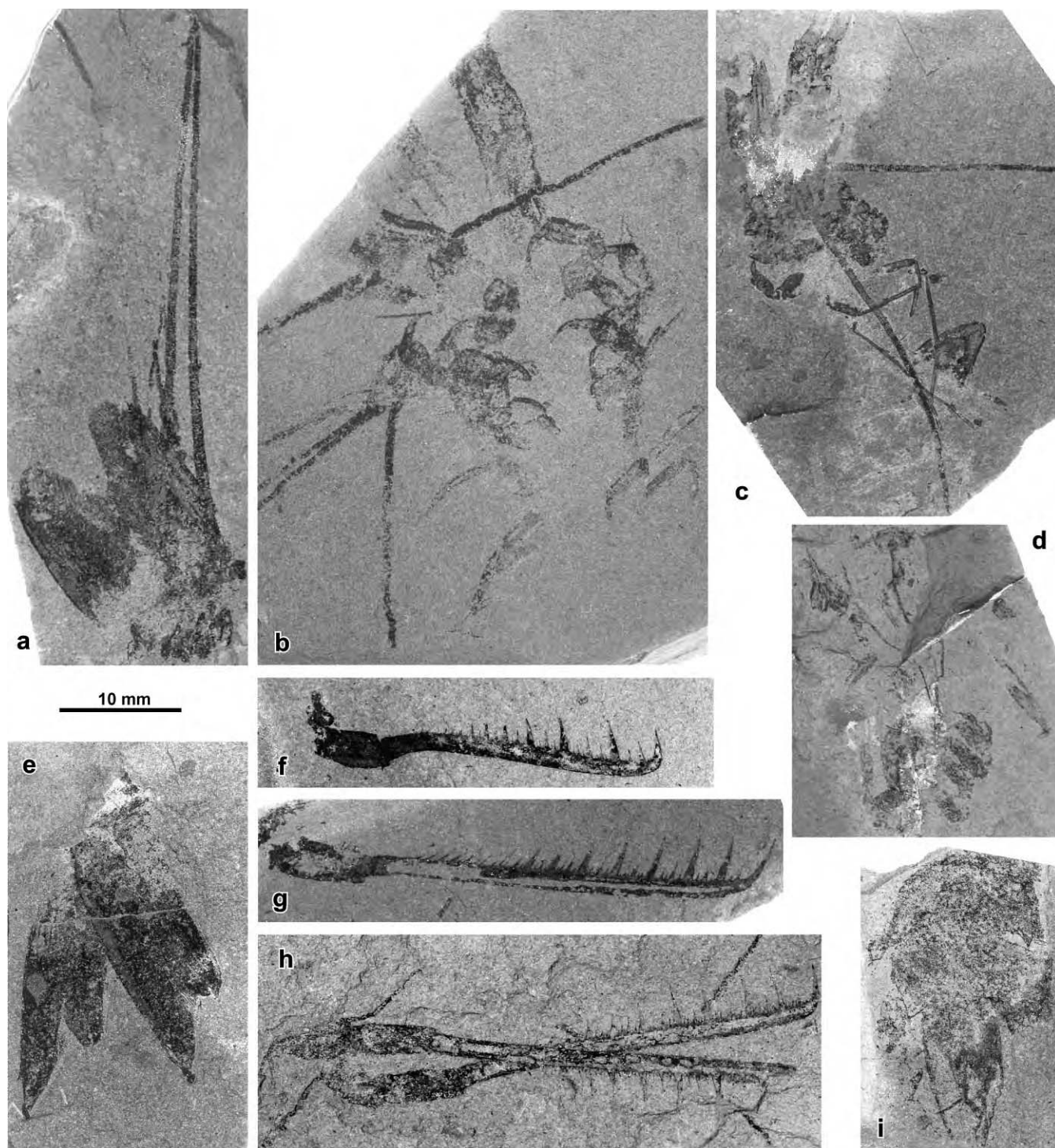


Figure 7 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; specimens photographed under alcohol: (a) NMNH 530448a, see Figure 6h; (b) NMNH 530458b, see Figure 8a; (c) NMNH 530459a, see Figure 9a; (d) NMNH 530439a, see Figure 6g; (e) NMNH 530446b, see Figure 9e; (f) NMNH 530461a, see Figure 6e; (g) NMNH 530455, see Figure 6f; (h) NMNH 530453a, see Figure 6d; (i) NMNH 530444a, see Figure 9f.

5.1.1. Paired maxillipeds Maxillipeds are sometimes found in pairs, i.e. of right and left sides, and occasionally even occluded (Figs 2, 4b, 6d). These may safely be presumed to have belonged to one individual of one species only. Of the 47 pairs collected, only 13 were adequately preserved for analysis. In these, no correlation could be found between the patterns of right and left rami. Each animal thus possessed either the characteristic patterns of two different species (as defined above), or of one of those species and one pattern that matches no described species: this was confirmed by statistical analysis.

5.1.2. Best-fit analyses. Each of the tooth patterns (i.e. each data set) recorded for the Nevadan material was compared with each of the four supposed species patterns cited above. Each set was compared several times with the pattern, in case the start of the tooth sequence did not coincide with the start of the pattern. The closeness of fit of a pattern to the tooth set was measured by the sum of square differences between each tooth in the pattern and the set: the smaller the sum, the better the fit. The shift needed to give the best fit between pattern and tooth set was thus found, the sum of the

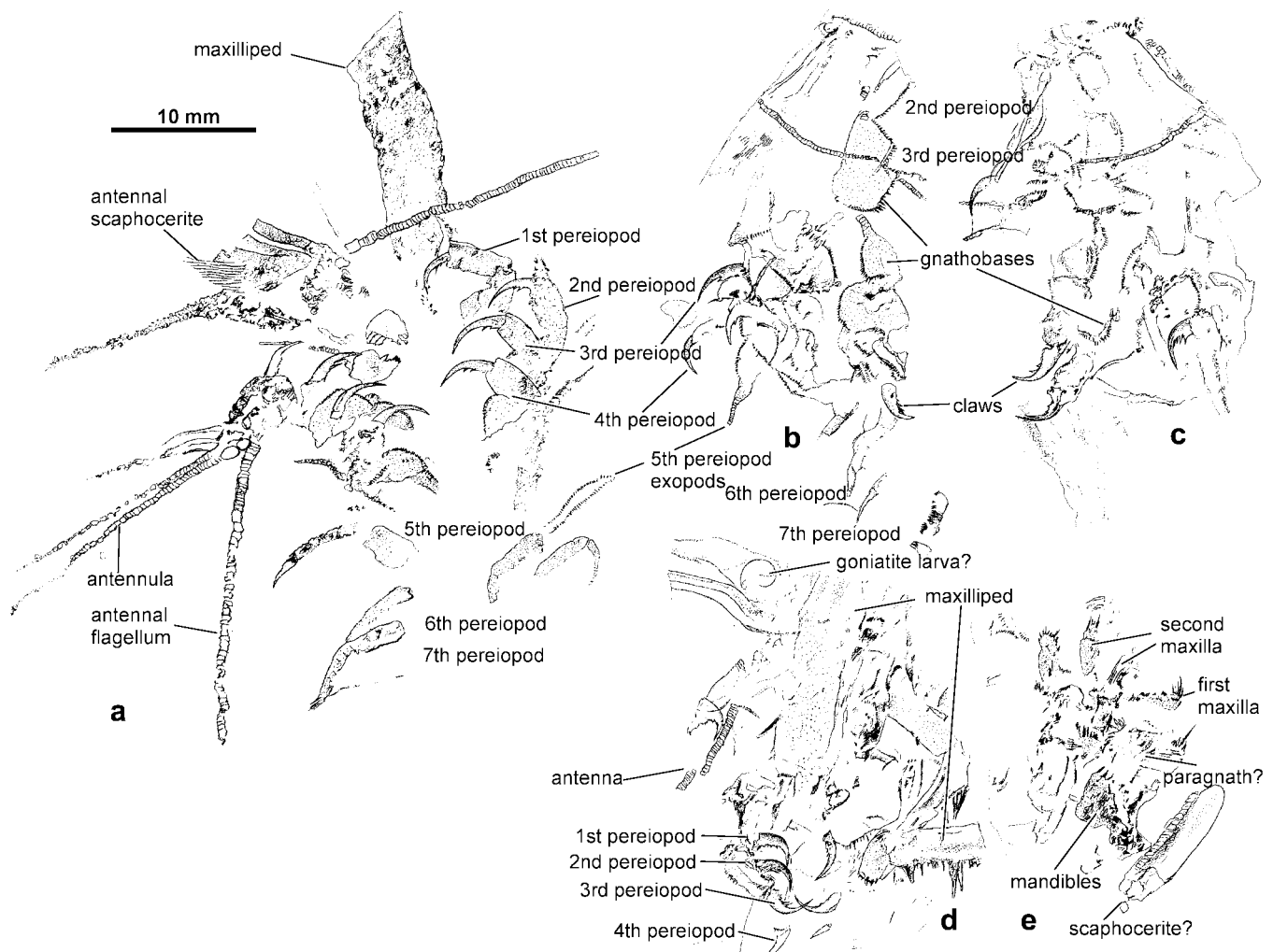


Figure 8 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; interpretative camera lucida drawings: (a) NMNH 530458b, see Figure 7b; (b, c) NMNH 530453b, part and counterpart, see Figure 5e; (d, e) NMNH 530451, latex replica of two associated specimens from different shale laminae, see Figure 5c, d. Scale bar applies to all images.

square differences recorded, and thereby a measure of the best fit between each set and the pattern was found. Overall, it was found that the fit of the teeth sets to the patterns was poor: a tooth set could fit just as well into one pattern category as another. There is therefore no statistical basis for reasoning that the teeth sets, at least in this case, fall into groups described by the four patterns suggested by previous researchers.

5.1.3. Bed by bed analysis. Samples (n=141 specimens) from different stratigraphic units or geographic areas were counted separately for species. Although *A. gracilis* continues to predominate in all samples, a high proportion of specimens could not be attributed to any existing species.

5.1.4. Conclusion. No difference has been identified between the sample from the Woodruff Formation of Nevada and the type species of the genus, *A. seriatus* Cooper, 1936, based on material from the probably coeval (Over 1992) Woodford Formation, Oklahoma. This is therefore the proposed species identification of the Nevadan material. The above evidence indicates that tooth pattern is not a reliable basis for discriminating between species of *Angustidontus*. Until other morphologic characters are identified to define other proposed species of the genus they should all be considered synonymous.

5.2. Taxonomic identity and affinities of the Polish material

No major differences from the Nevadan material can be discerned in the external morphology of the Holy Cross Mountains *Angustidontus*. As shown above, the Woodruff Formation sample is also hardly distinguishable from the Kentucky *Angustidontus seriatus*, *A. gracilis* from the Cleveland Shale, Ohio, or *A. moravicus* from the Ponikev Formation of Moravia. Apparently, the maxillipeds with delicate alternating denticulation characterise a whole plexus of species.

The only systematic difference between previous findings and the Polish material is the much smaller size of the latter's maxillipeds. That this is not necessarily a matter of local mortality pattern but rather a different mature animal's size, is suggested by the associated phosphatised mandibles. These are also consistently smaller than mandibles occurring in the same region but morphologically close to those from Nevada (although no identifiable mandible has yet been found in any articulated Polish specimen). Although the teeth pattern of the Wietrzna appendages is closely similar to that in Moravian or Nevadan specimens, this may not be significant. There seems to be an allometric change in their morphology (Fig. 15a) and extrapolation of the trend suggests that specimens from Nevada of size comparable to those from Poland, if available,

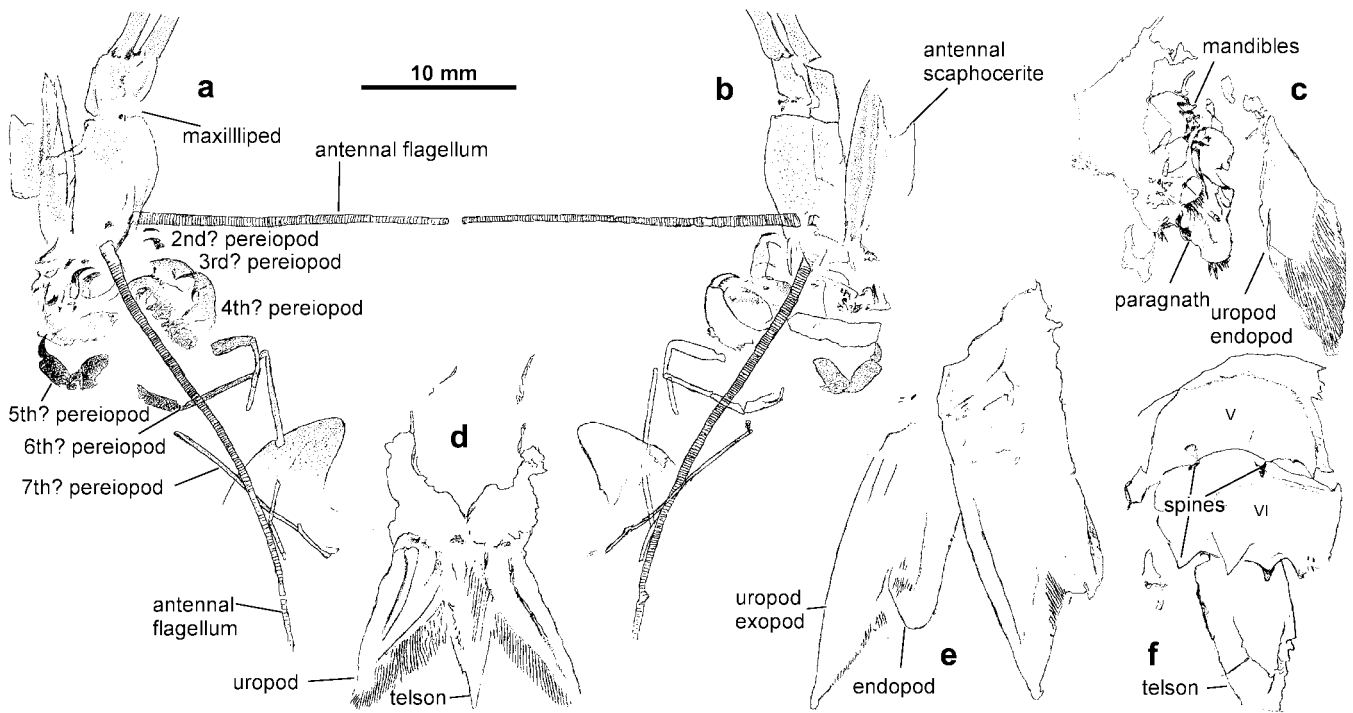


Figure 9 *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada; interpretative camera lucida drawings: (a, b) NMNH 530459a, part, see Figure 7c, and 530459b, counterpart; (c) NMNH 530452, see Figure 10c; (d) NMNH 530445a, see Figure 5g; (e) NMNH 530446b, see Figure 7e; (f) NMNH 530444a, see Figure 7i. Scale bar applies to all images.

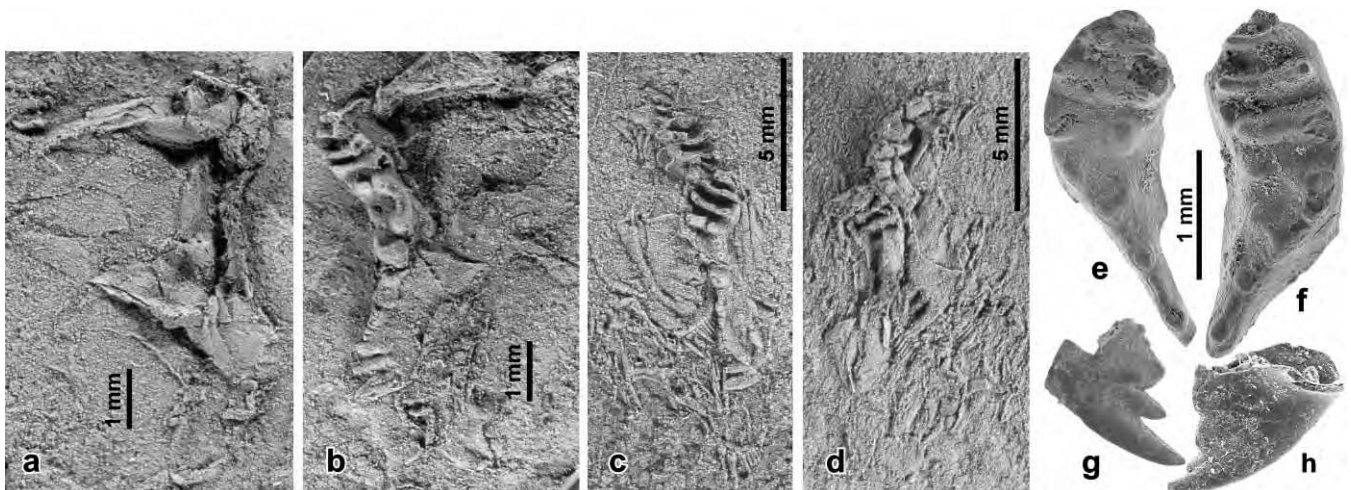


Figure 10 Mandibles of *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada (a–d; latex replicas) and the upper Famennian at Jablonna in the Holy Cross Mountains, Poland (e–h; phosphatised specimens): (a, b) NMNH 530460, part and counterpart; (c, d) NMNH 530452, part and counterpart, see Figure 9c; (e) ZPAL Cr 7/93, left mandibular coxal gnathobase in occlusal view from sample J-28; (f) ZPAL Cr 7/92, right mandibular coxal gnathobase, same sample; (g) ZPAL Cr 7/94, tip of left incisor part in lateral view, same sample; (h) ZPAL Cr 7/59, tip of right incisor part in posterior view, from sample J-35.

might be less elaborately denticulate. Unfortunately, the material studied is too fragmentary to support or dismiss this intuition.

Quite apparent are, however, the differences between mandibles of the Nevadan *A. seriatus* and those tentatively attributed to the *Angustidontus* from Wietrzna (Fig. 13b, d). As their association remains hypothetical, no formal species distinction is proposed. The Wietrzna species is here referred to in open nomenclature as *Angustidontus* sp. n. A. Fragmentary toothed appendages of the same age were also reported from the Knoppenbiessen beds in the Rhenish Slate Mountains, but of relatively large size for this species (Jux & Krath 1974).

The bearer of mandibles from the *Platyclymenia annulata* horizon at Kowala and Miedzianka, transitional in age and morphology between those of *A. seriatus* and *A. sp. n. A.*, is referred to as *Angustidontus* sp. n. B (Fig. 13c). The articulated shield and pleon from the same lithological horizon in the Rhenish Slate Mountains in Germany, included by Koch *et al.* (2003) as the paratype in their new genus *Suttropcaris*, may belong here (the holotype is a *Concavicaris* carapace with preserved compound eyes).

The possibility cannot be excluded that these three mandibular morphologies form an evolutionary succession, but there is no actual continuity in their stratigraphic distribution

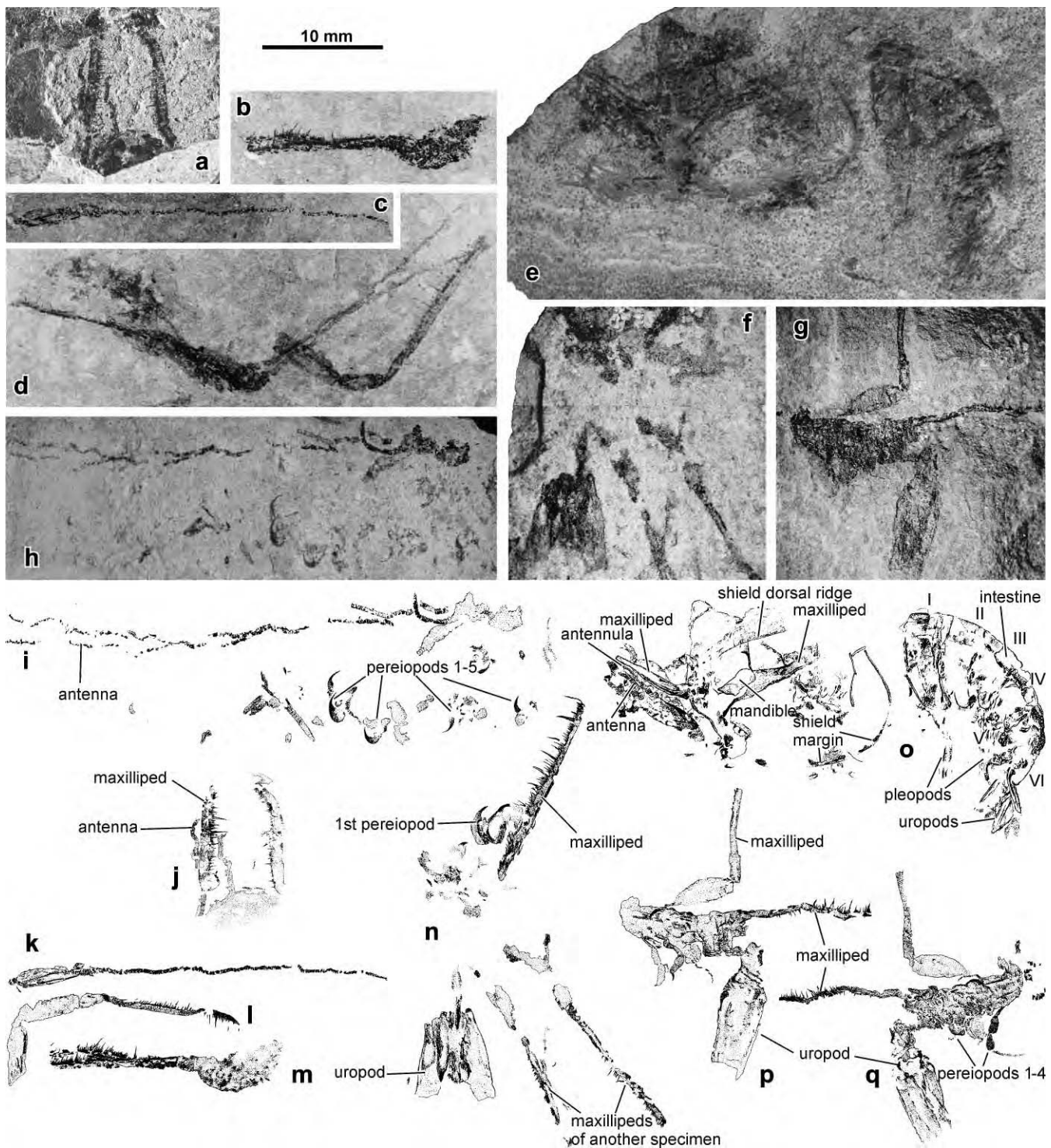


Figure 11 *Angustidontus* sp. from the early Famennian *P. crepida* Zone of the Holy Cross Mountains, Poland; except for (h) and (i), which is probably from Kowala, all specimens come from the Wietrzna quarry; photographs under alcohol (a–h) and interpretative camera lucida drawings (i–q). (a, j) ZPAL Cr 7/47, paired antennae, maxillipeds, and anterior part of the head in dorsoventral compression. (b, m) ZPAL Cr 7/5, laterally compressed pair of maxillipeds. (c, k) ZPAL Cr 7/56b, antenna with scaphocerite. (d) ZPAL Cr 7/9, antennae in association with maxillipeds. (e, o) ZPAL Cr 7/46, almost complete laterally compressed body. (f, n) ZPAL Cr 7/8, two sets of superimposed maxillipeds, one associated with probable 2nd pereiopod and tail fan. (g, p, q) ZPAL Cr 7/11, association of maxillipeds, pereiopods, and tail fan, part and counterpart. (h, i) ZPAL Cr 7/4, almost complete antennae associated with pereiopods. (l) ZPAL Cr 7/56c, almost complete maxilliped.

in the Holy Cross Mountains. The change would then be from a gnathobase bearing two transverse rows of denticles in the incisor part to an almost linear disposition of the incisor part and a more robust molar part (Fig. 13).

That the species diversity of the Famennian Angustidontidae was remarkable, is suggested also by the reinterpretation of the alleged decapod *Palaepalaemon newberryi* Whitfield by

Hannibal & Feldmann (1986; cf. Hannibal 1985). The new data on *Angustidontus seriatus* supports their proposal. There are apparent similarities also in the cephalothoracic shield morphology and in the structure of the anterior pereiopods. *P. newberryi* seems to be more robustly built and probably benthic as suggested by trace fossils attributed to this form (Feldmann *et al.* 1978). Its telson is wider, while the fringe of

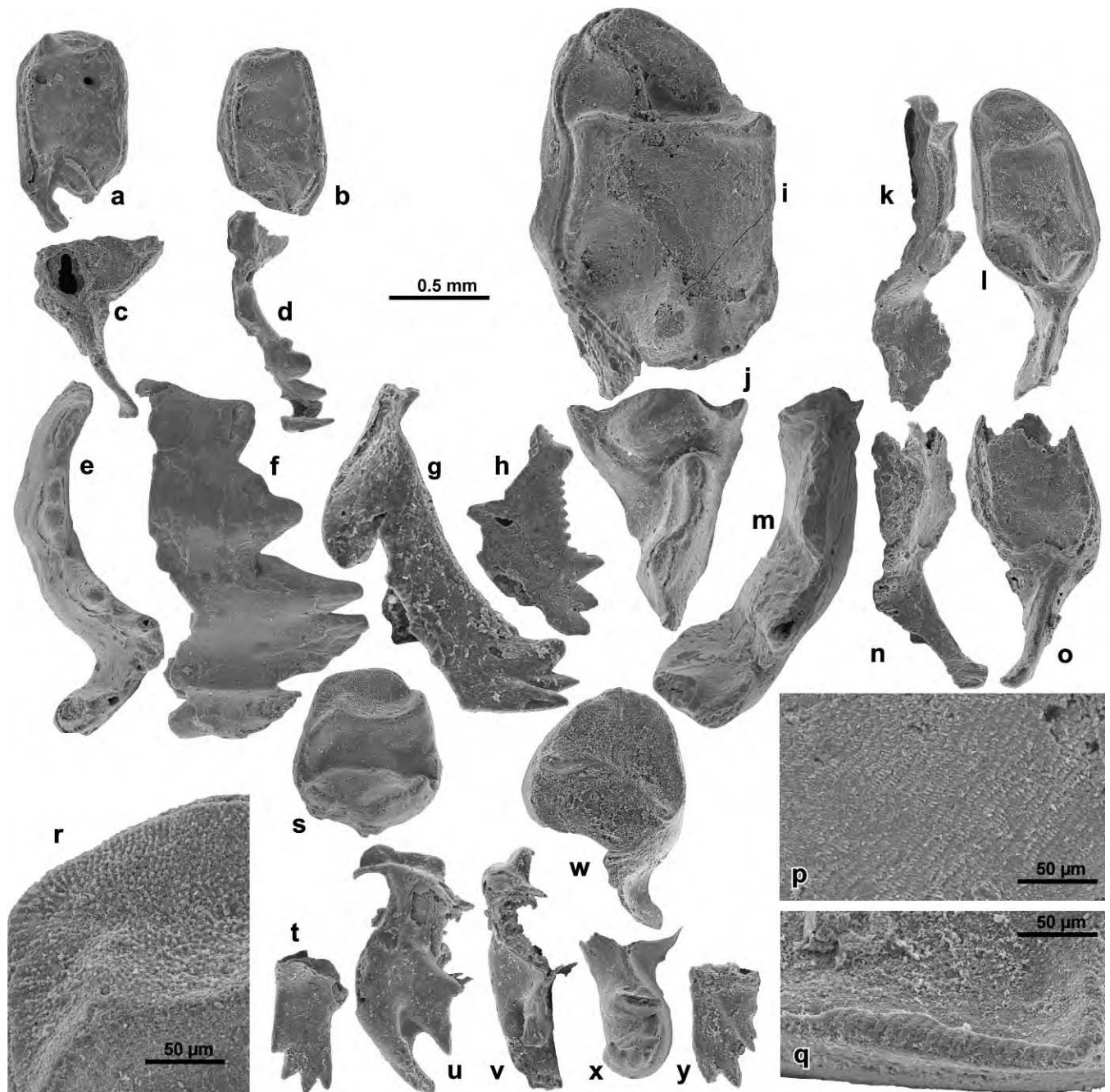


Figure 12 Chemically extracted phosphatised mandibles of *Angustidontus* sp. n. B. from the *P. trachytera* Zone (a–q) and *A. sp. n. A* from the *P. crepida* Zone (r–y) of the Famennian in the Holy Cross Mountains, Poland: (a) ZPAL Cr 7/82, molar part of left mandible in occlusal view, sample Ko-8a taken from the top of the *Platyclymenia annulata* event black shale at Kowala; (b) ZPAL Cr 7/79, same element and sample; (c, d) ZPAL Cr 7/77, incisor part and molar part bearing ‘*lacinia mobilis*’ of left mandible in occlusal view, same sample; (e, f) ZPAL Cr 7/85, incisor part of left mandible in occlusal and posterior views, sample Md-20, Miedzianka; (g) ZPAL Cr 7/76, incisor part of right mandible in posterior view, sample Ko-8a; (h) ZPAL Cr 7/91, incisor part of right mandible in posterior view, sample ŁS1-73–3, Łagów; (i, p) ZPAL Cr 7/88, molar part of right mandible in occlusal view (also magnified bases of setae), sample Md-18, Miedzianka; (j) ZPAL Cr 7/83, partial right incisor and molar parts in occlusal view, sample Md-29, Miedzianka; (k, l, q) ZPAL Cr 7/73, gnathobase of right mandible in occlusal views, sample Ko-20, Kowala, and also magnified setae of the molar; (m) ZPAL Cr 7/87, right incisor part in occlusal view, sample Md-18; (n, o) ZPAL Cr 7/75, right incisor part in posterior and occlusal views, sample Ko-8a; (r, s) ZPAL Cr 7/62, molar part of left mandible in occlusal view, and also magnified bases of setae, sample Wtr-21, Wietrznia; (t) ZPAL Cr 7/71, incisor part of left mandible in dorsal view, sample Ko-187, Kowala; (u, v) ZPAL Cr 7/58, almost complete mandibular gnathobase in posterior and occlusal views, sample J-35, Jabłonna; (w) ZPAL Cr 7/70, molar part of right mandible in occlusal view, sample Ko-187; (x) ZPAL Cr 7/61, incisor part of right mandible in occlusal views, sample Wtr-21; (y) ZPAL Cr 7/82, incisor part of right mandible in dorsal view, sample Ko-187.

uropodal setae is broader (Schram *et al.* 1978, text fig. 3; Hannibal 1985, fig. 1, but see his fig. 2 of Whitfield’s 1893 illustration). *Angustidontus* and *Palaeopalaemon* should not be separated at family level; one may even ask whether they

should be synonymised. This, however, must await better understanding of the morphology of *Palaeopalaemon*.

The pre-Famennian history of *Angustidontus* remains poorly known. As shown above, the maxillipeds of *Angustidontus*

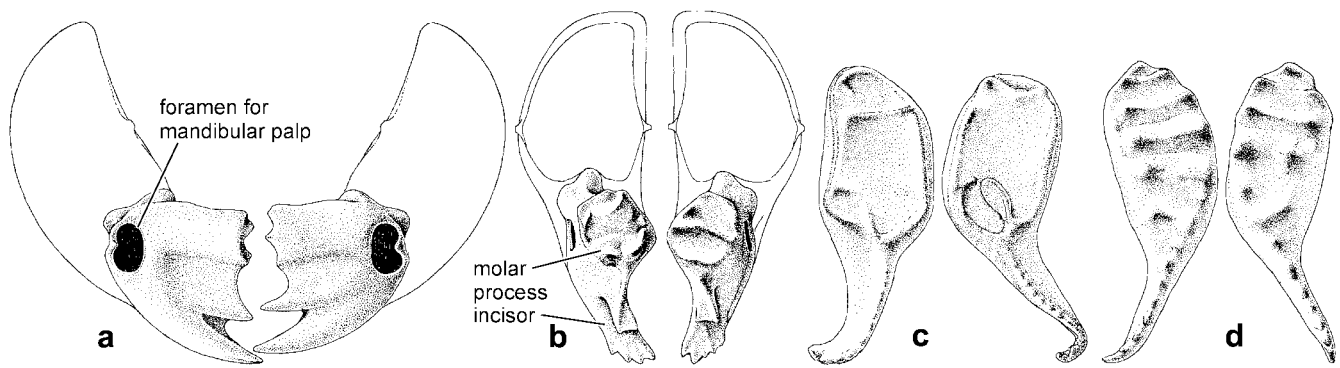


Figure 13 Restoration of mandibles of various *Angustidontus* species based on phosphatised specimens from the Holy Cross Mountains, Poland: (a, b) *Angustidontus* sp. n. A from the early Famennian; mandibles in posterior and occlusal views; (c) *Angustidontus* sp. n. B from the mid Famennian; mandible gnathobases in occlusal views; (d) *Angustidontus seriatus* Cooper, 1936 from the late Famennian; mandible gnathobases in occlusal views.

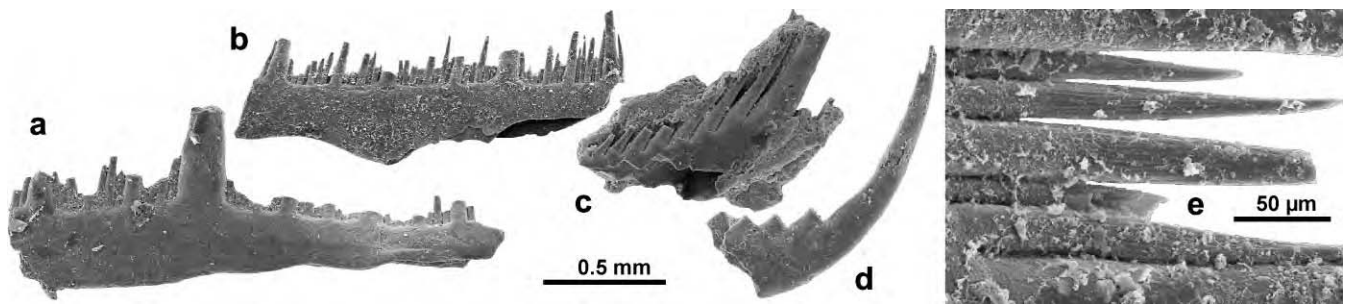


Figure 14 Micromorphology of phosphatised maxillipeds of *Angustidontus* sp. A. from the early Famennian sample Wtr-21, *P. crepida* Zone at Wietrznia in the Holy Cross Mountains, Poland: (a) ZPAL Cr 7/66, piece of the terminal article of the appendage from its midlength, showing a complex pattern of alternating tooth sizes; (b, e) ZPAL Cr 7/67, another finely toothed maxilliped, teeth magnified to show longitudinal striation; (c) ZPAL Cr 7/64, apex of the appendage with parallel arrangement of teeth; (d) ZPAL Cr 7/63, apex with gently curved terminal tooth.

weihmannae Copeland & Bolton, 1960 from the Frasnian Ireton Formation, Alberta (Copeland & Bolton 1960) fall within the variability range of *A. seriatus*. However, if it represents the typical morphology of its population, the rather robust appearance may be an expression of its relatively underived anatomy.

6. Evolutionary importance

Except for its specialised pereopodal appendages, *Angustidontus* is a generalised early eumalacostracan (Fig. 16), not much different from its Early and Middle Devonian predecessors (see Dzik *et al.* 2004). Remains of tergites of its anterior pereonites widely extending upwards suggest that the thoracic segments were not unified with the cephalothoracic shield: a clearly ancestral (plesiomorphic) character. It is typical of the peracarids and not known in extant eucarids but apparently characterised the Devonian ancestors of both clades. Also the greater length of the antennal flagellum than the antennular one is an underived character, placing *Angustidontus* below most of the peracarids, although this is also known in their underived Early Carboniferous members (e.g. Briggs & Clarkson 1985).

The functional differentiation of pereopods, the anterior four pairs being massive and armed with claws while the posterior three pairs are stenopodous, suggests affinities to the extant mysidaceans Eucopiidae or Petalophthalmidae. This seems to be a secondary (homoplastic) similarity, as molecular phylogenetic evidence points to the origin of the *Eucopia* lineage from gnathophausiids (Casanova *et al.* 1998; De Jong-

Moreau & Casanova 2001; Spears *et al.* 2005) having underived, morphologically uniform pereopods. An alternative interpretation of such differentiation of appendages in *Angustidontus* can be proposed by referring its possible ancestry to pelagic members of the anthracophausiid lineage (see Dzik *et al.* 2004). The stenopodous appearance would then be plesiomorphic and the grasping anterior thoracopods would have developed secondarily as a predatory adaptation, independently of the eucopiid and petalophthalmid mysidaceans.

The highly enlarged maxilliped of *Angustidontus*, with its toothed terminal article, is unlikely to have developed from a peracarid first maxilliped, which is invariably of minute size and functionally incorporated into the mouth apparatus. Instead, it is suggested that it originated from the first thoracopod of a pelagic filter-feeding ancestor with largely homonomous appendages, similar in general appearance to the Anthracophausiidae.

The aspect of the general body appearance making *Angustidontus* somewhat similar to the extant mysids, but not necessarily to their Palaeozoic ancestors, is the relatively short and weakly sclerotised shield. Such body proportions characterise also the ancestral Carboniferous stomatopods (see Jenner *et al.* 1998). The subchelate archaeostomatopod appendages are more complex than those of *Angustidontus*, so if their functional similarity results from common ancestry, it has to be looked for much prior to the Famennian.

The available evidence is obviously too incomplete to allow precise identification of the actual pattern of relationship among the early eumalacostracans. It seems, however, that *Angustidontus* may have its origin near the node from which

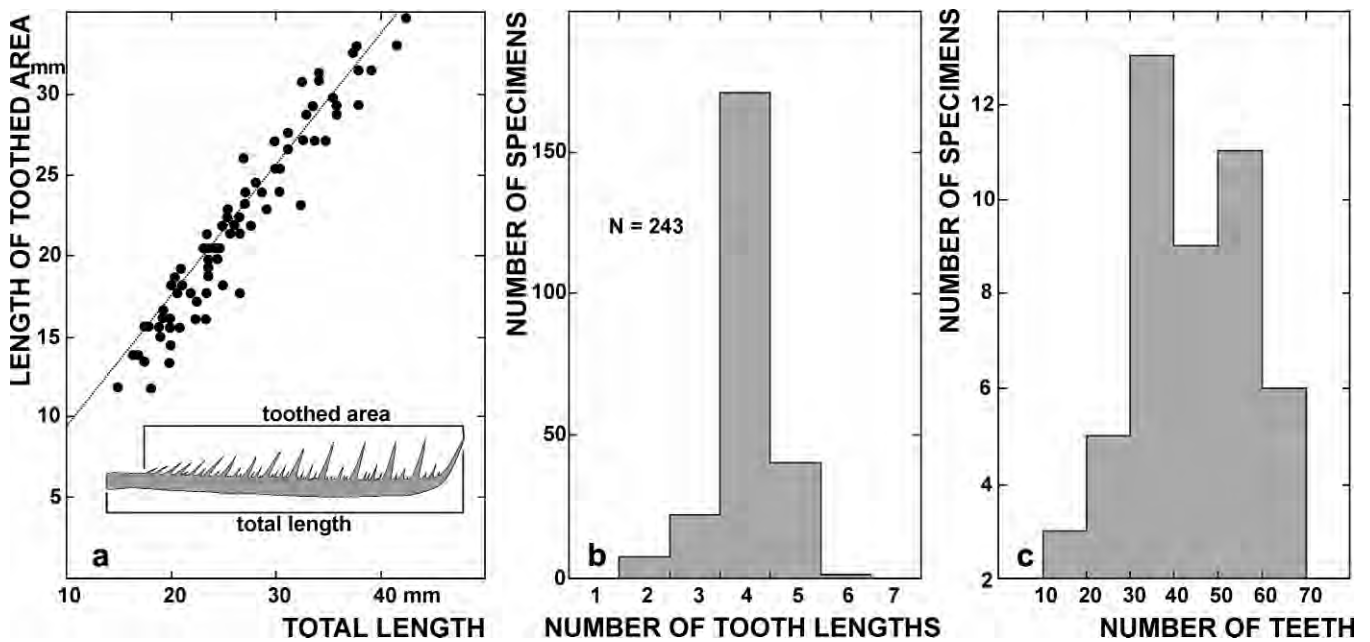


Figure 15 Sample of maxillipeds of *Angustidontus seriatus* Cooper, 1936 from the Famennian Woodruff Formation at Woodruff Creek, Nevada: (a) Ontogenetic change in extent of the toothed area of the maxilliped; note that in juveniles it is proportionally shorter; (b) Variability in complexity of the denticulation pattern as expressed by number of tooth lengths; (c) Variability in number of teeth.

the main eumalacostracan clades emerged, giving rise to the lineages of euphausiaceans, mysidaceans, and possibly also stomatopods. This is at least not in conflict with some anatomical data on extant members of these lineages (e.g. Richter & Scholtz 2001; De Jong *et al.* 2004).

7. Mode of life

The mode of life of *Angustidontus* can be assumed from environmental evidence offered by associated fossils or by interpreting its anatomy functionally.

7.1. Life environment

Angustidontus was a member of a community of low diversity but possibly of a rather high biological productivity. Many observers have noted the ubiquity of the characteristically toothed, distal article of these appendages, the maxillipeds, almost to the exclusion of other body parts. Thus, Smith & Ketner (1975, p. A31) record them as “the fossils most abundant and widespread, areally and stratigraphically, in the Woodruff [Formation] . . . with diligent search one can find them almost anywhere.” The fossil organisms associated with *Angustidontus* in Nevada, Poland, and Moravia are exclusively open sea pelagic (radiolarians, conodonts, cephalopods, entomozoid ostracods, concavicularids, fishes) or possibly epiplanktonic (*Sphenothallus* ‘worms’, *Guerichia* paper-thin bivalves). No undoubtedly benthic organisms have been found in the black shale richest in *Angustidontus* and *Concavicularis* specimens, although with the change to a more calcareous and not so bituminous laminated limestone, a low diversity benthos characteristic of soft muddy bottoms emerges. The bottom environment was probably anaerobic and poisoned with hydrogen sulphide, preventing decomposition of those crustacean cadavers, which fortunately for palaeontology settled on the bottom intact.

The concavicularids, pelagic ?crustaceans of unknown affinities (but see Vannier *et al.* 2006) associated with *Angustidontus*, had also subchelate appendages which flexed upwards at their midlength, and were armed with spines. They were efficient

predators, as shown by their stomach contents of cephalopod tentacular hooks, shark and teleost vertebrae, and fragments of thylacocephalan carapace (Pinna *et al.* 1985). Despite early interpretations to the contrary, there seems to be a consensus now that these were pelagic organisms, as advocated by Rolfe (1985). At least one specimen of a large *Concavicularis* from the Woodruff Formation has its grasping appendages preserved, but they were weakly sclerotised and only pale staining of the rock surface marks their appearance. They thus probably differed functionally from the appendages of associated *Angustidontus* and were probably designed to catch another kind of prey.

The recurrent association of crustacean predators so similar in size and appendage function requires another basis for discrimination of their ecological niches. One may surmise that, along with differences in prey, they occupied different, stratified levels in the water column.

7.2. Food

No taxonomically identifiable remains have been found in the gut contents of the studied specimens of *Angustidontus*. Some associated small pieces showing incremental growth may be cephalopod jaws or thin-shelled mollusc conchs. Near the mouth of specimen NMNH 530451 (Figs 5c, 8d) a spiral imprint suggestive of a goniatite larval conch occurs. Perhaps *Angustidontus* fed on cephalopods.

Among the Late Devonian pelagic animals known from fossils, conodonts are also likely prey for an animal equipped with such two-centimetre-long pectinate grasping devices. However, no recognisable conodont elements have been identified in the Nevadan material. The gut contents of the Wietrzna specimen ZPAL Cr7/46 (Fig. 11e, o) is transformed into an amorphous phosphorite. Perhaps undigestible mineral skeletons were discarded by the animal whilst processing the food with mouth appendages.

7.3. Functional analogues of toothed appendages

The toothed maxillipeds of *Angustidontus* resemble in their inferred subchelate mode of action the grasping appendages of

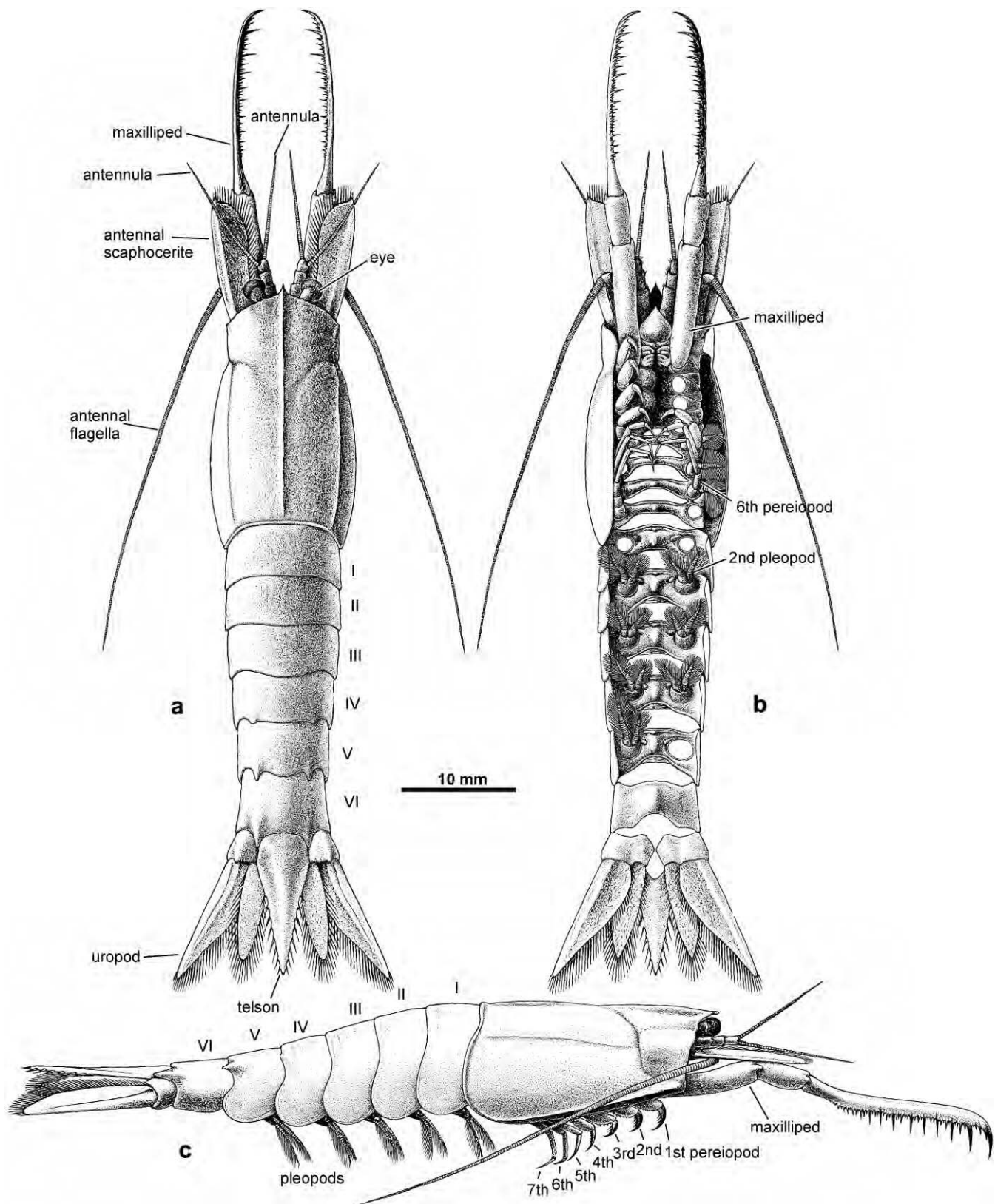


Figure 16 Restoration of the exoskeleton of *Angustidontus seriatus* Cooper, 1936 based on fossils from the Famennian Woodruff Formation at Woodruff Creek, Nevada in dorsal (a), ventral (b), and lateral (c) views. The shape of the labrum and details of pleopods are conjectural; the shape and proportions of the cephalothoracic shield may be somewhat distorted, being inferred from flattened specimens.

mantis insects and stomatopod crustaceans. As commented already above, the *Angustidontus* maxillipeds moved from upward down when folding, as in mantids, not down-up, as in spearing stomatopods. They may have acted as grasping and holding tools, but probably were not strong enough to cut the prey, unlike pterygotid eurypterid chelicerae (Selden 1984).

In general shape and alternation of sharp, long denticles, the *Angustidontus* maxillipeds closely resemble some elements of associated conodonts, namely S_3 elements of polygnathid conodonts. These elements were located anteriorly in the conodont mouth and their function was probably in catching and holding the prey (Jeppsson 1979; Dzik 1991). The conodont

apparatus is, however, an order of magnitude smaller than the maxillipeds of *Angustidontus*.

The tooth patterns of the pectinate chelae of decapod crustaceans *Thaumastocheles* (Nephropidae) and *Ctenocheles* (Ctenochelidae) seem analogous to those of the *Angustidontus* maxilliped. Groping over or raking through the seafloor with its opened and horizontally held claw has been suggested for the blind *Thaumastocheles* species (Green 1961). According to Tshudy & Sorhannus (2000) “direct observations of decapods bearing pectinate claws (i.e., chelae) have been few. Consequently, the adaptive significance of this claw form can be addressed only by speculation.” These analogies are of limited relevance if *Angustidontus* was an open-sea pelagic animal.

The distinctive pattern of alternating cycles of long and short teeth can be compared with similar patterns of dentition elsewhere among arthropods and fish. Such patterns characterise biting structures of animals that kill the prey by impaling them on long teeth, the intermediate shorter teeth serving to restrain the struggling prey and thus to prevent damage to the captor (Andrews 1985). The appendages thus match the paradigm for a fish-spear rather than a rake or comb. Further discussion of functional analogues is given by van Roy & Tetlie (2006).

Angustidontus probably did not survive the early Tournaisian, but already in the Viséan a eumalacostracan lineage of *Palaemysis* emerged, with a similarly toothed frontal appendage, probably filling the niche vacated by the extinction of *Angustidontus*.

***Palaemysis*.** The spinose frontal appendage of *Palaemysis dunlopi* Peach was originally identified as the second antenna (Rolfe in Wood 1982), with which Briggs and Clarkson (1983) concurred. They also compared it with the second thoracopod of stomatopods or to an extended maxilliped, which makes *Palaemysis* relevant to any consideration of *Angustidontus*.

Clark (1991) suggested the spinose frontal appendage was the mandibular palp, since he interpreted other appendages as first and second antennae. Restudy of the *Palaemysis* specimens illustrated by Clark (1991, figs 1a, 3D, 4F), together with other material, leaves no doubt that the spinose frontal appendage must be the modified flagellum of the second antenna. In Clark's (1991) figures 1a, 3D, the part labelled “A” to indicate what he interpreted as the proximal article of the “short second antennal flagella” is only a small part of the ‘top’ surface of the antepenultimate article of the spinose ‘frontal appendage’, of which otherwise most is broken away to reveal the external mould of the lower surface of that article. Thus reinterpreted, this specimen proves that the spinose ‘frontal appendage’ springs from the same basipod (shown at bottom of Clark's 1991 fig. 1a drawing) that bears the antennal scale. In Clark's (1991) figure 2C, the actual insertion of the purported second antenna “A” cannot be discerned, and thus provides no evidence as to the nature of this appendage. We agree with Clark's reinterpretation (pers. comm. 6 October 2005) that this may be the multiarticulate distal part of a pereopod. Clark's (1991) figure 4F specimen resembles that illustrated by Briggs and Clarkson (1983, text-fig. 3c), as well as other Granton specimens we have studied at the Royal Museum of Scotland. It shows the spinose frontal appendage inserting on a basipod along with the antennal scale, but in this case accompanied by a first antenna (projecting out of the picture, to the right). The presence of several detached ‘units’ of right and left spinose frontal appendages, together with their closely adjoined antennal scales (e.g. Briggs and Clarkson 1983 text-figs. 3b, c; plate 20 figs 3,4), argues for the original organic connection of these parts.

The superficial similarity of the *Palaemysis* spinose frontal appendage to the maxilliped of *Angustidontus* is thus due to convergence: both appendages were doubtless raptorial, although Schram (1986, p. 559) has suggested such structures indicate fossorial, tube-dwelling habits.

8. Conclusions

Angustidontus is an archaic (eocarid) eumalacostracan with an enlarged first pair of thoracopods homologous to the first maxillipeds of higher eumalacostracans. The pectinate terminal podomere of this grasping device acted by folding downward to strike, hold the prey, and to prevent it from wriggling free. The next four pairs of thoracopods, short and armed with strong terminal claws and serrate gnathobases, probably tore the prey apart and transported it to the mouth, with its strong mandibles. The tooth pattern of the maxilliped is too variable to be of taxonomic importance, although this is the most commonly fossilised part of the *Angustidontus* body. Mandibular gnathobases, frequently phosphatised and occurring in conodont samples, may prove to be of more taxonomic value. The body plan of *Angustidontus* suggests its phylogenetic position near the euphausiacean-mysidacean stem, with possible distant affinities also to the stomatopods. It probably originated from a pelagic ancestor, with thoracopods adapted to filtration and with locomotory abdominal appendages, by adaptation of the anterior thoracopods to a predatory function.

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