

THE SILURIAN TRILOBITE *ONYCOPYGE* WOODWARD

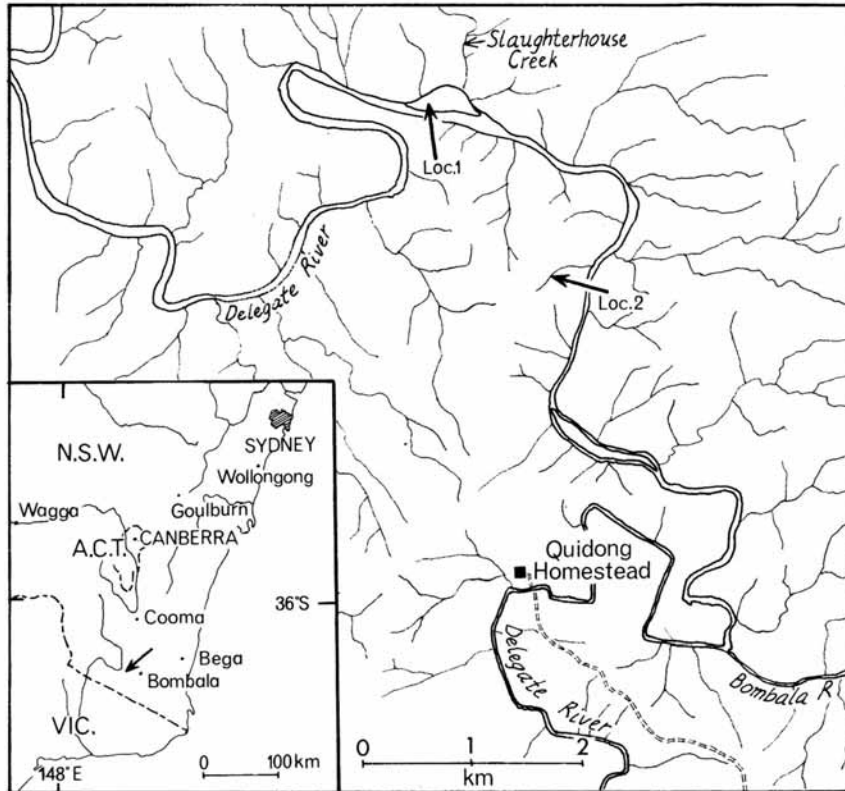
by D. J. HOLLOWAY and K. S. W. CAMPBELL

ABSTRACT. New material of *Onycopyge liversidgei* Woodward, from the Upper Silurian in the vicinity of the type locality at Quidong, New South Wales, permits the clarification of the morphology of the genus and its assignment to the Subfamily Deiphoninae. Another occurrence of the genus in Ludlovian rocks at Canberra is reported. Two types of pygidia at Quidong suggest that the species may be sexually dimorphic. Evidence is produced in support of the view that members of the Deiphoninae were benthonic.

THE trilobite *Onycopyge liversidgei* Woodward has been known only from a single specimen collected late last century by Professor A. Liversidge from a locality cited by Woodward (1880) as in 'the Silurian rocks of Bombala, New South Wales'. However, there are no Silurian rocks at Bombala, the nearest ones being at Quidong, 22 km to the west. New material of this species has recently been discovered in that area from the Ludlovian Quidong Formation (Brunker *et al.* 1971), which consists of an unknown thickness of mudstones, siltstones, and limestones. None of the specimens are in the same matrix as the type specimen. Associated with the new material is a rich and varied assemblage of brachiopods, bivalves, gastropods, trilobites, and ostracods, of which the most abundant elements are *Howellella nucula* (Barrande), *Atrypa* sp., *Molongia* sp., *Brachyprion* sp., *Salopina* sp. aff. *S. lunata* (J. de C. Sowerby), *Leptaena depressa* (J. de C. Sowerby), *Anodontopsis australis* Etheridge, and *Encrinurus* sp. aff. *E. mitchelli* Foerste (Tassell 1972). The specimens are in a hard siltstone, much of which has been naturally etched to yield internal and external moulds. The material of *Onycopyge* is completely disarticulated and often broken, and no hypostome, rostral plate, or thoracic segments have been found. Librigenae are mostly separated from cranidia, although some incomplete cephalons have been found. Often the bulbous part of the glabella is crushed or flattened but otherwise there is little apparent distortion.

The holotype (B.M. I 107) is a rather poorly preserved, almost complete individual with the exoskeleton of the thorax preserved. The thoracic axis has been destroyed, the pygidium badly broken, and the cephalon has been broken away to expose the external mould of the antero-ventral surface of the glabella and the ventral surface of the hypostome.

How much of this Woodward understood is not clear. His reconstruction suggests that he mistook the hypostome for the posterior part of the glabella, and hence believed that the cephalon was preserved in an inverted position. His footnote (p. 97) suggests that he belatedly appreciated his error, but did not alter his text, which still refers to the glabella as 'attenuated behind' (although the posterior part of the glabella is not preserved), and the small fixigenal and librigenal spines as 'directed forwards and upwards' (although they are directed slightly forwards and downwards).



TEXT-FIG. 1. Localities at which *Onycopyge liversidgei* Woodward was collected at Quidong, near Bombala, N.S.W. Locality 1, grid reference FV803181; locality 2, FV813163, Bombala Sheet 8724, Australian 1:100,000 Topographic Survey.

Whittard (1934) gave a much more satisfactory account of the species based only on the holotype which by that time had been better prepared. He also had access to the counterpart of the cephalon which showed the forms of both glabella and genae. It is his reconstruction that appears in Figure 341(10) of the *Treatise on Invertebrate Paleontology* (Moore 1959).

Because of the vague locality given for the holotype, the fact that it is preserved in a 'splintery limestone' whereas our new material was found in siltstone, and the absence of so many important morphological features in the holotype, we have been in some doubt about the assignment of our specimens to *O. liversidgei*. However, those features that are preserved are entirely comparable and we consider it better practice to adopt a conservative approach.

SYSTEMATIC DESCRIPTION

Family CHEIRURIDAE Hawle and Corda, 1847

Subfamily DEIPHONINAE Raymond, 1913

Genus *ONYCOPYGE* Woodward, 1880

Type species. Onycopyge Liversidgei Woodward, 1880, p. 98, from the Ludlovian at Quidong, N.S.W.

Diagnosis. Glabella in front of lateral glabellar lobe 1p greatly inflated, unfurrowed. Glabellar lobe 1p reduced to a slight swelling lying in the junction of the axial furrow and the broad depression behind the inflated part of the glabella. Axial furrow deep, directed antero-laterally adjacent to the postero-lateral edge of the inflated part of the glabella where apodemes 1p and 2p lie close together, but shallows rapidly opposite the palpebral lobe. Fixigena triangular, extended into a strong genal spine which at its base bears a stout, ventro-laterally directed spine on its ventral surface. Palpebral lobe inflated, with downturned lateral border. Librigena small, triangular, bearing a broad, ventro-laterally directed spine opposite γ . Posterior border of cephalon with a narrow articulating flange originating opposite the axial furrow and extending almost to an exsagittal line through δ . Hypostome deeply convex, with subtrapezoidal middle body.

Thorax of nine segments; pleurae consisting of an inner, unfurrowed portion with anterior and posterior articulating flanges, and an outer, free, backwardly curved, spinose portion, the two being separated by a low, knob-like tubercle on the dorsal surface.

Pygidium large, with 8-10 axial rings plus a terminal piece; first ring highly convex (sag. and tr.), more strongly curved anteriorly than the more posterior ones. First and second segments extended into strong, backwardly curved spines; postero-lateral border with a third pair of short, postero-ventrally directed spines; pleural region behind the second segment with variably developed pleural bands.

Remarks. In the original description Woodward (1880) noted the similarity between *Onycopyge* and *Deiphon*. Whittard (1934) realized that it also had a close relationship to *Sphaerocoryphe*, although he did not consider the stratigraphic ranges of the genera when he suggested that *Deiphon* 'could have evolved almost directly from either *Onycopyge* or *Sphaerocoryphe*' (p. 526). Öpik (1937) first placed *Onycopyge* in the Subfamily Deiphoninae together with the other two genera, and since then several authors have followed this approach (Prantl and Přibyl 1948; Henningsmoen, in Moore 1959). Lane (1971) removed *Onycopyge* from the Deiphoninae and in fact did not even regard it as a cheirurid. His reasons were threefold—his belief that the swollen part of the glabella comprises the frontal lobe only; the presence of a transverse furrow near the posterior border of each thoracic segment, which he maintained is not found in any cheirurid; and the larger number of axial rings in the pygidium.

The first two of these reasons are based on misconceptions. As is shown below, the swollen part of the glabella does contain lobe 3p and at least part of 2p. The transverse furrow on the thoracic pleura is the one that separates the pleural band from the posterior articulating flange, and is present on most cheirurids, including members of the Deiphoninae. Lane (1971, pl. 13, figs. 1, 5, 7a, b, and 12) has illustrated it for *Sphaerocoryphe*, and our investigations show that it is also present on *Deiphon*, albeit in a much reduced (tr.) form. In fact *Onycopyge* has both anterior and posterior articulatory flanges, features necessary for the type of articulation found in all cheirurids, in which there is no process-and-socket at the fulcrum but an anterior cavity is juxtaposed to a posterior cavity on the next segment. Although there is a process on the anterior edge of the segments of some genera (the flange process of Bergström 1973) this is really only the slightly expanded outer rim of the

anterior cavity which, during enrolment, slips inside the rim of the cavity on the segment in front.

This leaves only the number of rings in the pygidium to be considered. In his discussion of the taxonomy and phylogeny of the Cheiruridae, Lane placed considerable emphasis on the number of thoracic and pygidial segments, the family itself being diagnosed as having 9–12 thoracic segments and 1–4 pygidial rings. The Deiphoninae was defined as having 9 thoracic segments and 4 pygidial rings. *Onycopyge* is entirely comparable with members of this subfamily not only in gross morphology but also in such details as the pitting of the fixigenae, the shape of the librigenae, the presence of one secondary spine on the librigena and another on the fixigena, the segmental pattern of the glabella, the furrowing and articulation of the thoracic pleurae, and the development of large marginal spines from the first and second pygidial segments. It should also be noted that although Lane (p. 58) records only two pairs of pygidial spines on *Sphaerocoryphe*, Webby (1974) has described a species that has a third pair similar in position, shape, and orientation to that of *Onycopyge*, and Shaw (1968, pl. 13, fig. 23) figures similar spines on at least the early holaspids of *S. goodnovi* Raymond. Thus a very good case would have to be argued to exclude *Onycopyge* from the subfamily on the basis of the number of pygidial rings alone, especially as many other trilobite families are known to be very variable in this character (the Encrinuridae, for example) or to include an occasional genus with an unusual number of rings (the Cyclopygidae, for example).

Lane (p. 58) suggested that *Onycopyge* may be related to the Encrinuridae, though no reasons for this assessment were offered. Woodward, in the original work, had noted a similarity to *Staurocephalus*, a genus that many authors include in the Encrinuridae. We are unable to detect any close similarities with any member of the Encrinuridae. Moreover, even using Lane's criteria of number of thoracic and pygidial segments (which we cannot accept), it is difficult to see why *Onycopyge* is more closely related to the Encrinuridae than to the Cheiruridae.

We conclude that the affinities of *Onycopyge* are with the Deiphoninae, and in fact see no reason why the genus should be excluded from this subfamily. This conclusion requires that the definitions of the Cheiruridae and the Deiphoninae given by Lane (1971) be amended.

Within the Deiphoninae, *Onycopyge* is more closely related to *Sphaerocoryphe* than to *Deiphon*. (We accept the view that *Hemisphaerocoryphe* Reed is probably a synonym of *Sphaerocoryphe*.) This judgement is based on similarities between *Sphaerocoryphe* and *Onycopyge* in the size of the genae, the secondary ventrally directed spines on the genae, the distance between the articulatory fulcra, the size and shape of the thoracic pleural spines, and the general pattern of the pygidium. *Deiphon* is unique in the degree to which the genae are reduced, the width of the articulatory flanges decreased, and the pygidium posterior to the first segment modified. In view of the known stratigraphic ranges, these data imply the relationship shown below. The history represented by the dotted line remains unknown.

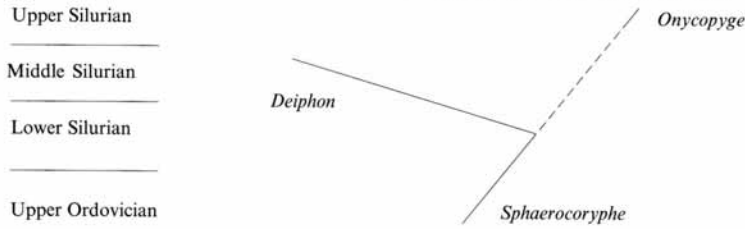
*Onycopoge liversidgei* Woodward, 1880

Plate 58, figs. 1-17; text-figs. 2A, B

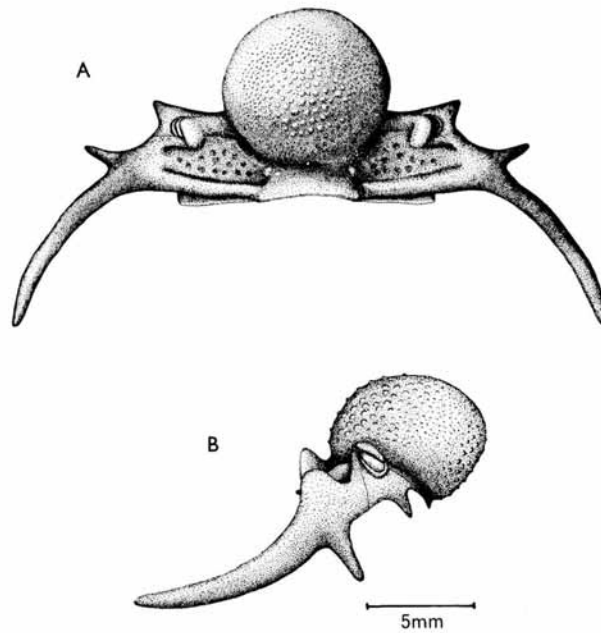
1880 *Onycopoge liversidgei* Woodward, p. 98.1934 *Onycopoge liversidgei* Woodward, Whittard; p. 521, pl. 16, figs. 10, 11; text-fig. 1b.

Material. Holotype BM I 107. British Museum (Natural History) Collection. Other material 21668a-b, 28990a-b, 28991a-b, 28992a-b, 28993a-f, 28994a-c, 28995a-b, 28996a-b, 28997a-b, 28998-28999, 29000a-d, 29001a-b, 29002, 29003a-b, 29004a-b, 29005a-b, 29006a-b, 29007, 29008a-b, 29009-29012, 29014. Geology Department, Australian National University Collection.

Description. Cephalon (excluding genal spines) with greatest width across the posterior border. Inflated part of glabella subspherical in dorsal view (for orientation see discussion below), rises vertically or sometimes slopes slightly backwards from the preoccipital depression, and steeply from the axial furrow just in front of apodeme 1p; anterior lobe extends beyond anterior border by about one-third its length. Anterior border furrow deeply impressed medially, giving a beak-like appearance to the anterior border in lateral view, but shallows laterally towards the axial furrow. Anterior border of cephalon vertical.

Occipital ring about three-fifths the width (tr.) of the widest part of the glabella, strongly convex (tr. and sag.), sloping forwards to merge with the posterior part of the median glabellar lobe in the preoccipital depression (see discussion below), and curving downwards into apodemal pits at its antero-lateral borders. Occipital apodemal pits elongate, transverse; occipital furrow not clearly defined medially. Preoccipital depression very deep, arcuate, and U-shaped in section.

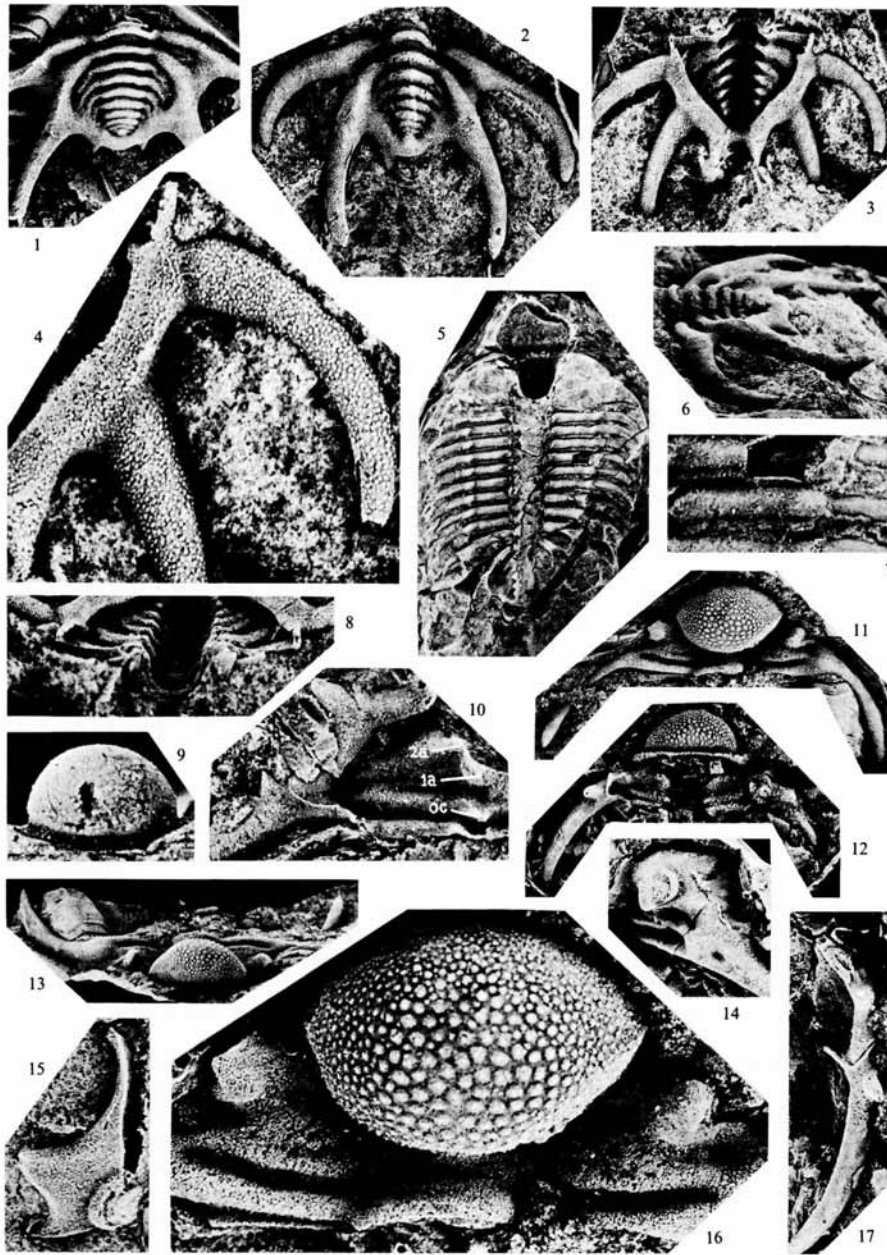
Palpebral lobe elongated parallel to axial furrow, bounded posteriorly by a broad, shallow, rounded furrow originating about half-way between the axial furrow and ϵ , deepening laterally and terminating in a rounded depression situated antero-laterally to the end of the posterior border furrow. Facial suture cuts the lateral margin behind the midpoint (exsag.) of the palpebral lobe and well in front of the posterior ventral spine, then swings back and on the ventral surface curves sharply around the base of the genal spine; ω - ϵ slightly sigmoid, rises sharply on to the palpebral lobe; ϵ situated opposite apodeme 2p and below the downturned rim of the palpebral lobe; plane containing ϵ - δ - γ slopes slightly downward anteriorly; γ - β directed anteriorly, falling sharply away from the palpebral lobe; β - α gently arcuate inwards, running subparallel to the lateral border so as to isolate a long, anterior, spine-like projection on the librigena, and meeting at a large angle with the rostral suture, which is approximately equal in width (tr.) to the occipital ring. Visual surface of eye crescentic, bounded below by a convex rim which, together with the downturned



TEXT-FIG. 2. Reconstruction of the cephalon of *Onycopye liversidgei* Woodward in dorsal view (A), and lateral view (B).

EXPLANATION OF PLATE 58

Figs. 1-17. *Onycopye liversidgei* Woodward, 1880. 1, latex cast of the broad type of pygidium, dorsal view, $\times 3$; ANU 29006b. 2, 6, latex cast of the narrow type of pygidium, dorsal and dorso-lateral views, $\times 3$; ANU 29003a. 3, 4, 8, latex cast of the narrow type of pygidium, ANU 29003b. 3, ventral view. The small projections on the doublure opposite the first pair of lateral spines are due to breakage of the original, $\times 3$. 4, enlargement of part of 3 to show the surface ornament, $\times 9$. 8, antero-ventral view showing the downturned ends on the anterior articulating flange, $\times 5$. 5, 7, plaster replica of the holotype, BM I 107. 5, dorsal view, $\times 1.5$. 7, enlargement of part of 5 to show the anterior and posterior articulating flanges on the thoracic pleurae, $\times 5.5$. 9, internal mould of the glabella, antero-ventral view, showing the rostral suture, $\times 6.5$; ANU 29011. 10, latex cast of the postero-lateral part of a cephalon, ventral view; free cheek in position but partly obscured; oc indicates the occipital apodeme; 1a, 2a indicate apodemes 1p and 2p respectively. Facial suture retouched, $\times 4$; ANU 29004a. 11, 13, 16, latex cast of the cranidium, ANU 28994c. 11, dorsal view, $\times 2$. 13, antero-dorsal view, $\times 2$. 16, enlargement to show the posterior articulating flange, palpebral lobes, and ornament on cheeks and glabella, $\times 6.5$. 12, latex cast of the cranidium, ventral view, $\times 3$; ANU 29014. 14, latex cast of cheek, dorso-lateral view, showing the eye, $\times 3$; ANU 29004b. 15, latex cast of the free cheek, dorsal view. The slender, spinose portion is directed anteriorly, $\times 6.5$; ANU 28995b. 17, latex cast of the genal spine and part of the cheek, ventral view, showing the facial suture, $\times 3$; ANU 28992a.



HOLLOWAY and CAMPBELL, *Onycopye* Woodward

rim on the palpebral lobe, gives the impression that the visual surface is surrounded by a convex border.

Posterior border strongly convex (exsag.), gently arched transversely, expanding slightly towards the genal angles, and lower than the surface of the librigena. Posterior articulating flange originates as a short (exsag.) ridge behind the axial furrow, expanding slightly until it is about one-half the length (exsag.) of the posterior border distally, and terminates with a hook about two-thirds the way along the posterior border. Posterior border furrow relatively long (exsag.), rounded in section, folded downward into the occipital apodemal pit proximally, expanding slightly in the vicinity of the base of the genal spine where it terminates, not meeting the lateral border furrow. Lateral border furrow very shallow, appears to terminate in the depression at the end of the post-ocular furrow. Lateral border strongly convex, high, increasing sharply in height at the base of the genal spine. Genal spine arcuate in both dorsal and lateral profiles. Glabella with pustules that are coarsest medially in the postero-dorsal region and above the anterior border; each major pustule with a secondary one at its apex. Genae ornamented with shallow pits in a triangular region bounded posteriorly by a low, smooth ridge adjacent to the posterior border furrow, and by fainter ridges parallel to the axial and palpebral furrows. Genal spines and posterior border densely and uniformly granulated.

Hypostome (described from cast of holotype) with middle body longer (sag.) than wide, expanding anteriorly, and with a faint, arcuate middle furrow originating in the lateral furrow about three-quarters of the distance from the front of the middle body, delineating a crescentic posterior lobe. Maculae not observed. Neither anterior nor posterior border preserved on the holotype, but the narrow posterior furrow remains. Anterior wings poorly preserved, but lie opposite the anterior margin of the middle body. Surface of hypostome obliterated.

Thorax (described from cast of holotype) with nine segments. Thoracic axis narrow, approximately one-sixth the total width of thorax, tapering slightly posteriorly. Axial rings not preserved. Inner portion of pleurae gently convex (exsag.), nearly horizontal, straight (tr.), parallel-sided, with very wide (tr.) anterior and posterior articulating flanges which are slightly downturned at their distal ends. Spinose portion of pleurae a little longer than articulated portion, flattened in section, gently tapered, directed downwards at about 30° to the plane of the inner portion, and curving uniformly postero-laterally. Surface of pleurae granulated, similarly to the genal spines.

Pygidium, apart from the marginal spines, subpentagonal in outline; axis bullet-shaped in outline; axial furrow clear, slightly impressed at the ends of the axial rings, but transgressed by the ring furrows. First axial ring inclined slightly forwards, expanding slightly towards the axial furrow, and bounded behind by a sharply incised furrow; articulating half ring approximately as long (sag.) as the ring proper; articulating furrow clearly defined, well-rounded at its base. Second axial ring of similar dimension to the first, and with a strongly developed pseudo-half ring that is distinguishable across the entire width of the axis. Next four or five rings of approximately the same sagittal length, but subsequent ones rapidly diminishing; pseudo-half rings weakly developed on the third, fourth, and fifth rings of some specimens. Anterior articulatory flange on the pleura of the first segment increasing gradually in length (exsag.) distally; an unfurrowed pleural band expands rapidly towards

the lateral border where it is humped and flexed, and then produced into a long, posteriorly-curving spine; in lateral view, spine slightly flexed ventrally at first, then reflexed dorsally towards its extremity. Second segment with pleural band much more posteriorly directed, exhibiting a similar humping across the border, and produced into a spine somewhat larger than that of the first segment. Between the first and second pleural bands is a furrow with a faint transverse swelling composed of the posterior articular flange of the first pleura and the anterior flange of the second. First two marginal spines almost circular in cross-section and slightly constricted on the ventral side where they join the pygidium proper. The more posterior segments with rapidly decreasing and progressively more posteriorly curving pleural bands separated by furrows of similar dimensions; the last two or three segments without clearly distinguishable pleural bands. A pair of short postero-ventrally directed marginal spines present near the posterior extremity; these spines ovate in cross-section. Border clearly defined, well-rounded, and bearing a slight medial terminal hump. Doublure narrows markedly towards the antero-lateral corner of the pygidium, slightly flexed outwards between the first two pairs of spines, and deeply embayed and arched postero-medially. Doublure and dorsal surface, apart from furrows, finely granulated. Apodemes well developed on all except the most posterior segments and are antero-medially elongated.

Remarks. As far as can be determined from the material available the species is quite constant in the characters of the cephalon, but there appear to be two distinct forms of pygidia—one with a narrow axis and narrow pleural region, the other relatively much broader. The observed differences are real, and cannot be explained in terms of distortion.

The narrow form has a strongly arched axis which is subtriangular in cross-section. The furrows on the pleural regions of segments 3–8 are short, later ones being strongly arched backwards so that the intervening pleural bands are tapered at their distal ends. The last furrow that retains a linear form is directed postero-laterally. The spine on the second segment is of about the same diameter as that on the first segment. The posterior spines are rather robust and postero-ventrally directed. The pygidium on the holotype, although only poorly preserved as a mould of the ventral surface, appears to be of this form.

In the broad form the axis is broader, more gently convex, and more rounded in cross-section. The axial rings are proportionately shorter (sag. and exsag.). The furrows on the pleural regions of the segments behind the second are longer, the pleural region being broader, and the difference in curvature between earlier ones and those on later segments is not as marked. The last distinguishable furrow curves more strongly backwards at its distal end than the corresponding furrow on the narrow pygidium. The spines on the second segment of the broad form are slightly stouter than those on the first segment, and diverge at a greater angle than the corresponding spines on the narrow form. Furthermore, one specimen of the broad type (ANU 29006) has 10 axial rings rather than the usual 8. One other specimen of this type has 8, but it is of a rather small holaspid, while the only other specimen available, although larger, is incomplete. Only 8 rings can be counted on this specimen but there could be more present.

All specimens of the broad type of pygidium are from the one locality, while at the other locality only the narrow type occurs. However, one specimen of the narrow type was recovered from the former locality. Whether these differences are due to sexual dimorphism or to the presence of two subspecies is uncertain. From Bohemia, Alberti (1971) has also recognized broad and narrow forms of the pygidium of *Cheirurus* (*Crotalocephalus*) cf. *pauper* Barrande, which he interprets as sexual dimorphs. It may also be of significance that *Deiphon barrandei* Whittard has two types of pygidium that can be readily distinguished by the form and orientation of the posterior pair of spines. The differences have been attributed to size by Whittard (1934) and Lane (1971). The figured specimens fall clearly into one type or the other, there being no mention of intermediates. They possibly indicate dimorphism.

Recently, distorted specimens of a cranidium and two pygidia have been recovered from the Ludlovian Riverside Formation at Canberra. The pygidia are of interest in that, although they represent small holaspids and are poorly preserved, they seem to have only six axial rings plus a terminal piece.

MORPHOLOGICAL NOTES

In the above description there are two points that require some explanation.

1. The furrow forming the posterior margin to the inflated part of the glabella in the Deiphoninae was interpreted by Lane (1971, p. 58) as 'a combined occipital and 1S furrow'. The relationship between the first glabellar furrows and the occipital furrow is not clear in *Deiphon* and *Oncopyge*, in which the glabella posterior to the inflated portion has been greatly shortened relative to that of some species of *Sphaerocoryphe*. In *Sphaerocoryphe* glabellar lobes 1p are small, subtriangular, slightly raised structures, isolated by furrows 1p that join with the occipital furrow medially, the latter occupying *only the posterior part* of the broad furrow behind the inflated portion of the glabella. This is quite obvious in many species of this genus figured by Shaw (1968) and Lane (1971) and it would seem to imply that at least part of the furrow in question was a depressed part of lobe 2p.

The ideal way to test this implication would be through an ontogenetic study, but no complete growth stages of a deiphonine are known. It seems clear from other cheirurids, however, that the part of the glabella between the inner ends of the isolated lobes 1p is part of lobe 2p, and this is confirmed by a study of *Acanthoparypha chiropyga* Whittington and Evitt (Whittington and Evitt, 1954, pl. 28, figs. 31-44). In the protaspis of that species the glabellar furrows are more or less complete, but during the meraspis stages the furrows become incomplete medially, furrows 1p become oblique and almost join the occipital furrow to isolate lobes 1p. Lobe 2p expands posteriorly and comes into contact medially with the occipital furrow, as can be demonstrated by the progressively more posterior movement of the paired tubercles associated with the glabellar lobes in successive ontogenetic stages.

In the case of the Deiphoninae, some support for this point of view is obtained from the meraspis of *S. goodnovi* Raymond figured by Shaw (1968, pl. 13, fig. 18), which is very similar to the meraspis of *Acanthoparypha*.

Hence the median portion of the depression forming the posterior margin of the inflated part of the glabella is neither a true glabellar furrow nor an expanded occi-

pital furrow, but an occipital furrow plus part of a median glabellar lobe. In view of the fact that furrow 2p is not developed, the extent to which lobe 2p is involved cannot be determined. Nor is it always possible to distinguish the extent of the occipital ring. Hence we prefer to use the term *preoccipital depression* for the depressed medial part of the glabella in front of the occipital ring and behind the inflated lobe. Although the structures of this region are less clear in *Deiphon* and *Onycopyge*, there are such obvious similarities between these genera and *Sphaerocoryphe* that the same terminology should be applied.

2. For purposes of description and functional interpretation, it is necessary to decide upon the relaxed, unrolled posture of these organisms. The nature of the thoracic articulations, the shape of the axial rings, and the length of the articulating half rings, suggest that the thoracic pleurae and the pleural regions of the pygidium would have been more or less coplanar. Using the same arguments with respect to the cephalon, it is clear that the relaxed position would have been with the plane containing the posterior margin of the occipital ring approximately vertical. In this orientation the visual field would have an appreciable anterior component. These comments apply to *Deiphon*, *Sphaerocoryphe*, and *Onycopyge*. We have used the above orientation in our description.

MODE OF LIFE

Previous authors (Staff and Reck 1911; Ruedemann 1934; Whittard 1934) have regarded *Deiphon* as planktonic, basing this interpretation on features such as spinosity and the swollen glabella which, they argued, could have contained a low-density fluid to aid flotation. Whittard (1934) extended the interpretation to *Onycopyge* and *Sphaerocoryphe*. Recent plankton have acquired a variety of adaptations to aid flotation, some of which—such as storage of oil droplets in the protoplasm—we can have no knowledge of in fossil material. However, those adaptations involving variation in skeletal morphology can be identified in fossils.

These adaptations, which are usually aimed at the increase of the $\frac{\text{surface area}}{\text{weight}}$ ratio, can be summarized as follows:

- (1) the development of fine spines;
- (2) the reduction of the thickness of the skeleton;
- (3) the small size of the organism;
- (4) the development of globose chambers to contain low-density body fluids;
- (5) the development of all-round vision.

Many of these comments are applicable also to entirely nektonic crustaceans, though some of these reach a much larger size.

The question now is to determine the extent to which the members of the *Deiphoninae* exhibit these characteristics. *Deiphon* itself certainly has developed a highly spinose skeleton, but whereas recent pelagic crustaceans become spinose by the production of extensions of the normal body, in *Deiphon* the spines result from skeletal reduction. For a trilobite of any given length this produces a decrease of surface area, and hence it should be compensated for by a proportionately greater decrease in weight. Whittard (1934, p. 527) was of the opinion that this was achieved.

It is true that there would be a large decrease in the weight of the soft tissue and the exoskeleton of the cephalon, but the totally enclosed pleural spines of both the thorax and the pygidium are proportionately increased in length, and this has a tendency to increase the weight of the exoskeleton per unit volume. Further, the exoskeleton remains quite thick—it is 0.35 mm thick at the base of a genal spine of maximum diameter 2.5 mm, and reduces to only 0.30 mm at a maximum spine diameter of 1.5 mm.

In size, *Deiphon* is certainly one of the smaller members of the Cheiruridae, but adults commonly attain a length of 25 mm whereas the majority of recent plankton are less than a centimetre in length and many do not exceed 2–3 mm (Raymont 1963).

The animal certainly had a wide visual field in both vertical and horizontal senses. Of course the glabella is inflated, and *may* have contained a substance of low density.

The bulk of this evidence is against the hypothesis that *Deiphon* was planktonic, and the remainder is inconclusive or cannot be checked. None of it specifically favours a nektonic mode of life either, though the total design does not favour the view that it was an active swimmer. In fact, if it could be shown that the glabella was inflated to contain an enlarged stomach rather than low-density material, the remainder of the morphology would be consistent with a predominantly benthonic mode of life. Some evidence on this point can be obtained from a study of the hypostome, which is considered below.

If the above arguments with respect to *Deiphon* are correct, then *Sphaerocoryphe* and *Onycopyge*, both of which are generally larger in size and have relatively un-reduced skeletons, are even less likely to be planktonic or nektonic. In fact there is little reason to believe that their mode of life was much different from that of members of the Cheirurinae.

The hypostome of *Deiphon* is a well-calcified structure, being as thick as the dorsal exoskeleton. In its normal position (i.e. with no gap at the hypostomal suture) the hypostome is inclined at a high angle to the horizontal plane (see orientation discussion above). This angle is so great that complete enrolment of the thorax and pygidium would be impossible; yet the animal could enrol, as is shown by the development of articular devices and normal articulating half rings on all segments, and by the embayments in the anterior border of the cephalon on either side of the hypostomal suture that received the posterior spines of the pygidium (Lane 1971, pl. 12, fig. 6*a, b*). The deep furrow across the anterior half of the hypostome probably also fitted into the doublure of the pygidium. This implies that the hypostome was able to rotate up under the glabella during enrolment. The rotational axis must have been through a point at each extremity of the hypostomal suture, a feature well brought out by the figures referred to above. Rotation would have been achieved either by the attachment of muscles to the anterior wings or from the body of the hypostome to the anterior part of the glabella (see Eldredge 1971).

The effect of this rotation would be to compress the oesophagus and probably the stomach when the animal was enrolled. An explanation has then to be offered for the function of the hypostome in the extended position. If the hypostome were capable of rotating while the animal was not enrolled, the system could act as a pump for sucking food into the stomach. This offers the possibility of an explanation for the expanded glabella. It also suggests a function for the ventrally directed

secondary spines on the genae. These together with the genal spines would have allowed the cephalon to rest sufficiently clear of the sea bottom to permit the hypostome to rotate. Presumably mud would have been ingested.

Sphaerocoryphe and *Onycopyge* had hypostomes of basically the same type as *Deiphon*, and presumably they functioned in the same way.

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