

BIVALVED ARTHROPODS FROM THE CAMBRIAN BURGESS SHALE OF BRITISH COLUMBIA

by D. E. G. BRIGGS

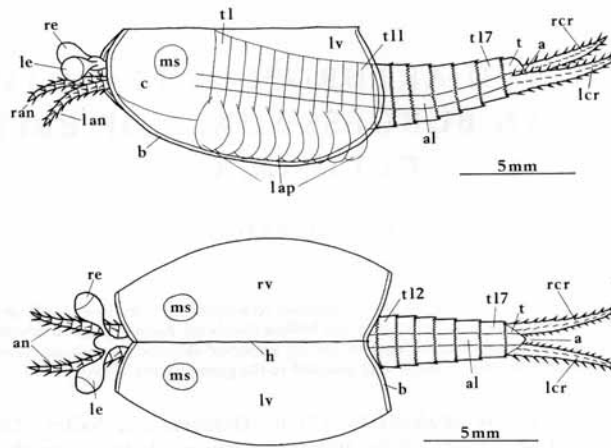
ABSTRACT. The new phyllocarid genus *Perspicaris* is proposed to include the type, *Canadaspis dictynna* Simonetta and Delle Cave, 1975, and *P. recondita* sp. nov., from the Middle Cambrian Burgess Shale of British Columbia. The two species are reconstructed in detail apart from the poorly preserved thoracic appendages. *Hymenocaris? parva* Walcott, 1912, from the same locality, is tentatively assigned to the genus *Tuzoia* Walcott, 1912.

THE material referred by Walcott (1912) to *Hymenocaris* Salter, 1853 is being re-examined as part of a study of the bivalved arthropods from the Burgess Shale. In this paper two of the specimens which he figured as *H.* (= *Canadaspis*) *perfecta* (1912, pl. 31, figs. 2, 4) are shown to differ in the morphology of the telson and cephalic appendages from the others, and are placed in a new genus *Perspicaris*. *Canadaspis dictynna* Simonetta and Delle Cave, 1975, is redefined and designated the type species. *Perspicaris*, although lacking a rostral plate and abdominal appendages, is assigned to the Phyllocarida. A reinterpretation of the only known specimen of *Hymenocaris? parva* reveals the spinose nature of the carapace border. The evidence is inadequate, however, to determine the genus, and it is referred with a query to the phyllocarid *Tuzoia*.

Terminology. The morphological terms used in the descriptions are those of Moore and McCormick (in Moore 1969) as far as possible; the telson is not considered to be a true somite. The sagittal plane is that passing vertically through the long axis of the body. The following symbols are used on the plates and text-figures: a, anus. ad, trace of carapace adductor muscle. al, alimentary canal. an, antenna. ap, appendage. b, border of carapace. c, cephalic region. cr, caudal ramus. e, eye. gu, gut contents. h, hinge line of carapace. is, inter-somite boundary. l, prefix indicating left side. ms, muscle scar on carapace. n, nodular feature. p, cephalic appendage? beneath the antenna of GSC 45280. r, prefix indicating right side. t, telson. t1, t2, etc., trunk somites numbered posteriorly (assuming a total of 17). v, valve of carapace. Breaks of slope are represented by hachures, the solid line at the upper edge of the break, the hachures directed downslope. Stippled areas represent 'outcrops' of matrix within the outline of a specimen, unless otherwise indicated. The evidence upon which the reconstructions are based is illustrated, as far as possible, by the plates. Differences in level on the fossils are expressed by a minute 'scarp' on the specimen which either casts a shadow, or reflects light, depending on the angle of illumination. The photographs, except Plate 67, fig. 4 and Plate 72, figs. 4, 5, were taken on fine-grained, 35-mm panchromatic film in ultra-violet radiation. The radiation was directed at approximately 30° to the horizontal except where reflection was desirable, when the angle was increased to about 65°. Plate 67, fig. 4, was taken on fine-grained, half-plate, orthochromatic film, in ordinary light directed at a high angle, the specimen immersed in white spirit. Plate 72, figs. 4, 5, were taken through a Wild binocular microscope, the specimen illuminated by an intensity lamp with a green filter. An interpretation of the specimens is presented where necessary as an adjacent camera lucida drawing. The specimens were rotated in relation to a unidirectional light source during the preparation of these drawings; different aspects of the morphology are revealed by varying the direction and angle of illumination (indicated in the plate explanations).

[Palaeontology, Vol. 20, Part 3, 1977, pp. 595-621, pls. 67-72.]

H



TEXT-FIGS. 1, 2. Reconstructions of *Perspicaris dictynna* (Simonetta and Delle Cave, 1975). 1, lateral view, features beneath the carapace tentative. 2, dorsal view.

Respositories. The following abbreviations are used: GSC—Geological Survey of Canada, Ottawa; ROM—Royal Ontario Museum, Toronto; SM—Sedgwick Museum, Cambridge; USNM—National Museum of Natural History, Washington, D.C.

Preservation. Whittington (1971, pp. 1180–1196, 1198, fig. 24) discussed the preservation of *Marrella splendens* in detail, explaining the effect of variations in orientation to the bedding prior to compaction on the appearance of the fossil. *Perspicaris* shows a similar range of configurations. Specimens orientated in *parallel* aspect, the sagittal plane normal to the bedding, preserve the cephalic appendages, valves, and the trunk and telson symmetrically arranged about the mid-line (Pl. 69, fig. 1). Specimens preserved in *lateral* aspect, the sagittal plane parallel to the bedding, show the valves approximately superimposed (Pl. 67, figs. 1, 2). Examples also occur in an intermediate or *oblique* aspect, the outline of one valve approaching completeness, the other folded beneath itself (Pl. 68, fig. 6; Pl. 69, fig. 3). All eleven identified specimens of *P. dictynna* appear to have been complete when buried. Poorly preserved individuals, however, particularly those lacking the telson, can not be assigned to the species as they might equally be juveniles of *P. recondita* or *Canadaspis perfecta*. Isolated valves within the size range are at least as common as complete individuals, but the majority are probably those of juveniles of *C. perfecta*. Only two of the twelve known specimens of *P. recondita*, on the other hand, approach a degree of completeness (Pl. 69, fig. 3; Pl. 70, figs. 1, 2), and five consist only of posterior trunk somites and the telson. Isolated carapaces are usually difficult to distinguish from those of *C. perfecta*. Five of the specimens of *P. dictynna* are preserved in *lateral* aspect, four in *parallel*, and two in *oblique*. The majority of specimens of *P. recondita*, however, are preserved in *parallel* or *parallel-oblique* aspect, possibly partly due to the influence of the flattened caudal furca, and only the carapace is known in *lateral* aspect (Pl. 72, fig. 3). The isolated carapace USNM 189244 (Pl. 72, fig. 7) approaches a *vertical-oblique* orientation to the bedding (cf. *M. splendens*, Whittington 1971, p. 1187).

SYSTEMATIC DESCRIPTIONS

Class MALACOSTRACA Latreille, 1806
 Subclass PHYLLOCARIDA Packard, 1879
 Order and Family uncertain
 Genus PERSPICARIS gen. nov.

Derivation of name. Latin: perspicax (sharp-sighted); caris (crab).

Type species. *Canadaspis dictynna* Simonetta and Delle Cave, 1975.

Other species. *P. recondita* sp. nov.

Diagnosis. Carapace with hinge line, valves sub-oval, tapering anteriorly, rostral plate absent. Pedunculate eyes large, borne on an elongate projection of the cephalon. Abdominal somites lacking appendages, telson not posteriorly produced, caudal furca spinose.

Geological horizon. Middle Cambrian, Stephen Formation, Burgess Shale section, *Bathyriscus-Elrathina* Zone, British Columbia.

Perspicaris dictynna (Simonetta and Delle Cave, 1975)

Plates 67, 68; Plate 69, figs. 1, 2; text-figs. 1-11

1975 *Canadaspis ovalis* (Walcott); Simonetta and Delle Cave *pars*, p. 12, pl. 5, fig. 3; pl. 40, figs. 22-24.

1975 *Canadaspis* sp.; Simonetta and Delle Cave *pars*, pl. 40, fig. 11.

1975 *Canadaspis dictynna* Simonetta and Delle Cave *pars*, p. 12, pl. 5, fig. 4; pl. 43, fig. 14.

Holotype. USNM 189280, part and counterpart (designated Simonetta and Delle Cave 1975), Plate 67, figs. 3-5, original of Simonetta and Delle Cave 1975, pl. 43, fig. 14.

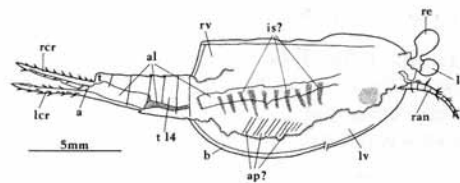
Other material. USNM 114244, 114254 with counterpart, 189242, 189245, originals of Simonetta and Delle Cave 1975, pl. 40, figs. 22, 24, 23, and 11 respectively; USNM 207245 with counterpart, 207246, 207247, 213804, 213833, and one additional specimen. USNM 213805 with counterpart, 213842 and 213850 may belong to the species.

Diagnosis. Furcal rami elongate, bearing a row of spines laterally, dorsally, and ventrally.

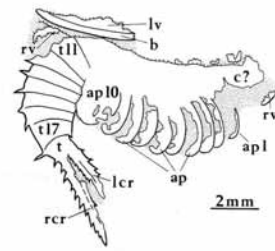
Locality and stratigraphical horizon. All the material bears the USNM locality number 35k, i.e. the 'Phyllopod bed' in the Walcott Quarry (see Fritz 1971, for an account of the stratigraphy). No specimens were collected by the GSC expeditions (Whittington 1971); no isolated carapaces were found which correspond in shape or size to that of *P. dictynna*. The fauna associated with the USNM specimens is confined to *Canadaspis perfecta*, *Waptia fieldensis*, *Sidneyia inexpectans*, *Pagetia bootes*, *Ottoia prolifica*, and unidentifiable fragmentary material, and affords no precise indication of the levels in the quarry from which they were obtained.

DESCRIPTION

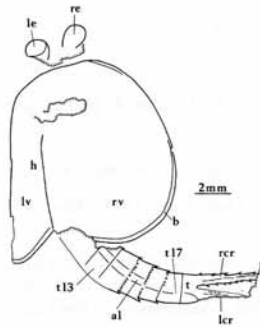
Cephalic region. The cephalon is poorly defined even when exposed by exfoliation of the carapace (Pl. 68, fig. 6), or the partial loss (Pl. 67, figs. 1, 2; Pl. 68, fig. 5), or removal (Pl. 67, fig. 4) of the overlying valves. The anterior margin is gently curved, convex anteriorly (Pl. 67, fig. 7; Pl. 69, fig. 2, ventral view) in parallel aspect, but only a suggestion of the margins is afforded by USNM 114244 (Pl. 67, figs. 1, 2) and 189280 (Pl. 67, fig. 4) in lateral aspect, and an accurate reconstruction of the outline is impossible. A pair of large,



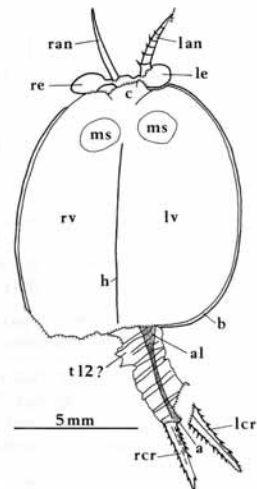
TEXT-FIG. 3



TEXT-FIG. 4



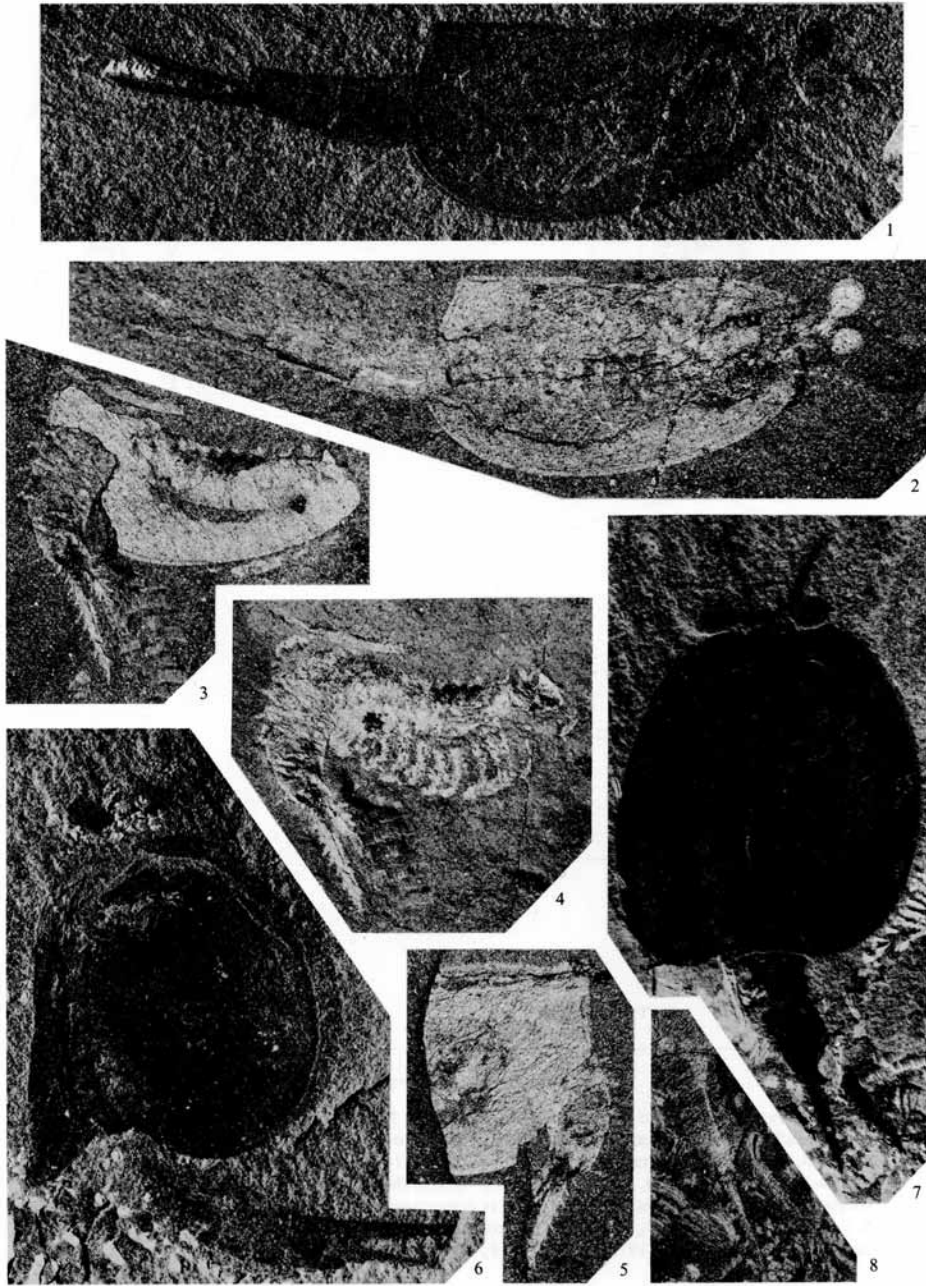
TEXT-FIG. 5



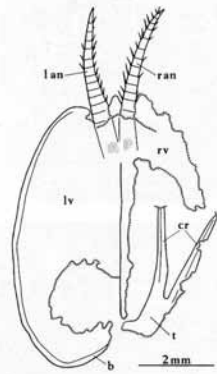
TEXT-FIG. 6

EXPLANATION OF PLATE 67

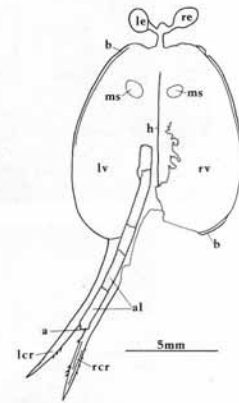
Figs. 1-8. *Perspicaris dictynna* (Simonetta and Delle Cave, 1975). 1, 2, USNM 114244, lateral: 1, east, $\times 5$; 2, north, reflected, $\times 5$; original of Simonetta and Delle Cave 1975, pl. 40, fig. 22; right valve largely missing revealing 'body' layer; text-fig. 3. 3-5, USNM 189280, part and counterpart, lateral: 3, east, reflected, $\times 5$; 4, north, alcohol, $\times 5$, right valve removed to reveal thoracic appendages; 5, north, reflected, $\times 5$; original of Simonetta and Delle Cave 1975, pl. 43, fig. 14; text-fig. 4. 6, USNM 207247, oblique, east, $\times 5$; text-fig. 5. 7, 8, USNM 189242, parallel, ventral aspect: 7, north, $\times 5$; 8, east, reflected, $\times 5$, showing abdomen and telson; original of Simonetta and Delle Cave 1975, pl. 40, fig. 23; text-fig. 6.



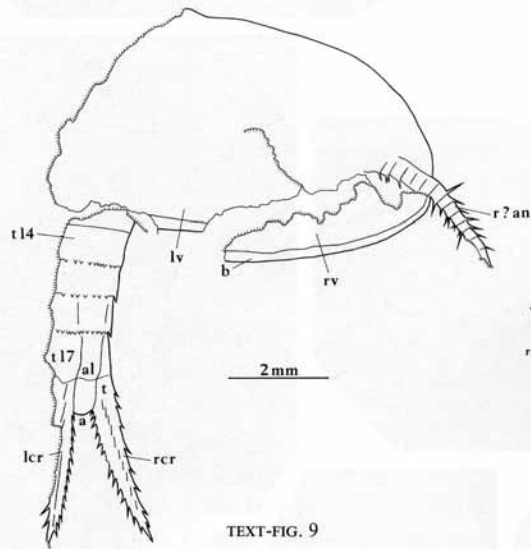
BRIGGS, *Perspicaris* from the Burgess Shale



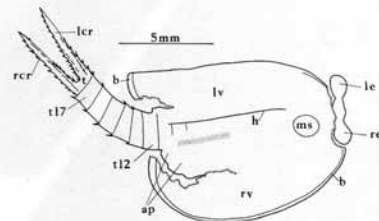
TEXT-FIG. 7



TEXT-FIG. 8



TEXT-FIG. 9



TEXT-FIG. 10

EXPLANATION OF PLATE 68

Figs. 1-7. *Perspicaris dictynna* (Simonetta and Delle Cave, 1975). 1-3, USNM 207245, part and counterpart, parallel: 1, north-east, $\times 5$, carapace partly removed revealing telson; 2, north, $\times 5$; 3, east, reflected, $\times 10$, showing antennae; text-fig. 7. 4, USNM 114254, parallel, north, $\times 5$, original of Simonetta and Delle Cave 1975, pl. 40, fig. 24b; text-fig. 8. 5, USNM 207246, lateral, west, $\times 10$, trunk apparently rotated through 90° so that the dorsal side is uppermost; text-fig. 9. 6, 7, USNM 189245, oblique: 6, north-west, $\times 5$; 7, north, $\times 10$, part of carapace removed to show traces of appendages; original of Simonetta and Delle Cave 1975, pl. 40, fig. 11; text-fig. 10.



BRIGGS, *Perspicaris* from the Burgess Shale

highly reflective, ovoid features (Pl. 67, fig. 2) borne on an elongate, distally expanding, projection of the cephalon are interpreted as eyes. They may be preserved superimposed on the anterior margin of the carapace (Pl. 67, fig. 7) or extending beyond it (Pl. 69, figs. 1, 2), suggesting that the projection was flexible. The eyes are suboval in outline in parallel (Pl. 68, fig. 4) and oblique aspect (Pl. 68, fig. 6), tapering slightly proximally, but subcircular in lateral aspect (Pl. 67, fig. 2). The highly reflective distal area preserved on some specimens (Pl. 67, fig. 2) may represent the visual surface; a defined subcircular area on the left eye of USNM 207247 (Pl. 67, fig. 6) may be similar in origin.

The cephalic region bore a pair of stout, elongate, segmented antennae attached ventral of the eyes (Pl. 67, figs. 1, 2). The antennae appear to have been subcircular in cross-section, tapering gradually distally and composed of at least fourteen segments (evident on USNM 207246, Pl. 68, fig. 5; USNM 207245, Pl. 68, figs. 1-3). The segments became more elongate towards the distal extremity of the appendage; individually they increased in cross-section distally, each one inserting into the anterior margin of that proximal to it. The anterior margin of the segments, apart from, apparently, the most distal, bore a fringe of elongate spines extending laterally a distance approaching the width of the segment (Pl. 68, figs. 3, 5). The antennae were flexible; they are preserved directed forward, curved to the left (Pl. 67, fig. 7) or right (Pl. 68, figs. 1-3), or downward (Pl. 67, figs. 1, 2). The maximum known anterior extent of the alimentary canal is preserved on USNM 213804 (Pl. 69, figs. 1, 2) but the trace terminates at a point which is probably posterior of the cephalon. There is no indication of the labrum. Two pairs of nodular features are preserved flanking the hinge line just posterior of the attachment of the cephalic appendages of USNM 213804 (Pl. 69, fig. 2). These nodes may result from the nucleation of pyrite (Whittington 1971, p. 1180). The posterior pair is elongate normal to the hinge and may indicate the posterior margin of the cephalon. The anterior pair are slightly elongate parallel to the hinge and may represent a paired cephalic organ such as the antennal nephridium.

Carapace. A bivalved carapace loosely covered the anterior part of the body, including the proximal parts of the antennae and eye stalk and part of the trunk appendages. Five trunk somites, in addition to the telson, are preserved extending beyond the carapace of USNM 114244, in lateral aspect (Pl. 67, figs. 1, 2) but this number varies from four (Pl. 68, fig. 5), or even less (Pl. 67, figs. 3, 5, presumably due to distortion), to six or seven (Pl. 67, fig. 6; Pl. 69, fig. 1). The carapace was apparently only attached to the anterior of the body; the greater part of the trunk could move independently of it (Pl. 68, figs. 4, 5). Dark, reflective, subcircular areas which occur in the anterior apices of the valves are interpreted as traces of muscle scars, and indicate that the attachment was cephalic. They have no apparent relief on the dorsal surface of the carapace, but are slightly raised on the ventral (Pl. 67, fig. 7; Pl. 69, figs. 1, 2). A crescentic, reflective area on the adaxial margin of the muscle scars of USNM 213804 (Pl. 69, fig. 2) may be a trace of the adductor muscle; its attachment to the body may be represented by a dark, reflective, subcircular area near the base of the antenna of USNM 114244 (Pl. 67, figs. 1, 2).

The valve was suboval in outline, tapering anteriorly and expanding slightly postero-ventrally. The anterior margin is usually obscured by exfoliation (Pl. 68, figs. 1, 6) or compaction against the cephalic appendages, but appears to have been gently rounded (Pl. 67, fig. 7). The hinge line is approximately straight in lateral (Pl. 67, figs. 1, 2) and parallel aspect (Pl. 68, fig. 4), but its anterior extension is unknown. There is no evidence that a rostral plate was present, but the hinge was produced very slightly posteriorly (Pl. 67, figs. 1, 2). The posterior margin of the valve diverged from the hinge line at an angle of about 110° (Pl. 67, figs. 1, 2), creating a shallow embayment between the valves (Pl. 68, fig. 4) similar to that at the anterior margin (Pl. 67, fig. 7). In the absence of evidence to the contrary the valves are assumed to have been joined by a band of flexible cuticle, which permitted variations in the degree to which they were approximated by the adductor muscles.

An indication of the original convexity of the carapace is provided by the relief of some specimens (Pl. 68, figs. 1, 2) and the concentric folds which parallel the ventral margin of the flattened valves (Pl. 67, fig. 7; Pl. 68, fig. 4). A wide border, sloping slightly abaxially, was bounded on its inner margin by a narrow ridge on both the exterior (Pl. 68, fig. 5) and interior (Pl. 67, fig. 7) surfaces of the valves. The carapace was smooth otherwise, apart from the muscle scars, and wrinkles and folds acquired during preservation (Pl. 68, fig. 5). The border appears to follow the hinge line on USNM 114244 (Pl. 67, figs. 1, 2) but this is not an original feature and may be the result of folding parallel to the hinge during compaction. There is no evidence that the border was sculptured, but this may be a function of the small size of the specimens.

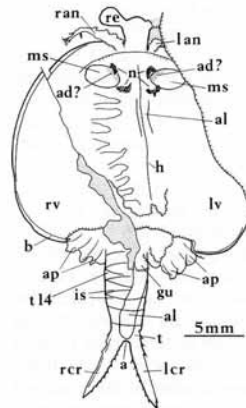
Trunk. The anterior somites of the trunk are usually obscured by the carapace, and removal of the latter (Pl. 67, figs. 3, 4), where feasible, has revealed little detailed evidence of their configuration. The 7 posterior-most somites of the trunk appear to have lacked appendages (Pl. 67, figs. 1, 2, 4; Pl. 68, fig. 7) although those of the preceding somites may be compacted against them. There appear to have been 10 appendage-bearing somites. The strongest evidence for this number depends on the assumption that each somite bore a single pair of appendages—10 limbs, presumably paired, were revealed by the removal of the right valve of USNM 189280 (Pl. 67, fig. 4). Extrapolation based on serially arranged, reflective traces on USNM 114244 (Pl. 67, fig. 2) and 213804 (Pl. 69, fig. 2) supports this figure. The trunk thus appears to have consisted of a thorax of 10 appendage-bearing somites and an abdomen of 7 somites, in addition to the telson. The somites are henceforth numbered posteriorly from 1 to 17 (see reconstruction, text-figs. 1, 2).

The height of the somites diminishes gradually posteriorly in lateral and oblique aspect (Pl. 67, figs. 1, 2; Pl. 68, fig. 7), this feature becoming more marked posterior of somite 16, and is greater in lateral (Pl. 67, figs. 1, 2) than in parallel (Pl. 68, fig. 4) or oblique aspect (Pl. 68, fig. 6) indicating that the trunk was suboval in cross-section. A series of dark, reflective bands on the thorax of USNM 114244 (Pl. 67, figs. 1, 2) probably represents traces of the inter-somite boundaries (cf. *Yohoia plena*, Whittington 1974) and indicates that the thoracic somites were much shorter (sagittally) than those of the abdomen. The latter appear to have increased slightly in sagittal length posteriorly but this may be obscured by the curvature of the trunk (Pl. 68, fig. 7). Traces of the abdominal inter-somite boundaries offset on opposite sides of the trunk are evident on some specimens (Pl. 69, figs. 1, 2). The posterior margin of each somite was fringed by up to forty short, stout spines (Pl. 68, fig. 5). The trunk was very flexible and is preserved curved to the right (Pl. 67, fig. 6) and left (Pl. 68, fig. 6), ventrally (Pl. 68, fig. 5; Pl. 67, figs. 3, 5), and even apparently curved through almost 180° beneath the carapace (Pl. 68, fig. 1; the trunk of this specimen may be disarticulated). Flexure was achieved by varying the degree of overlap along the inter-somite boundaries; the lateral margins of individual somites are shorter on the concave side of the trunk (Pl. 68, fig. 7; Pl. 67, figs. 3-5).

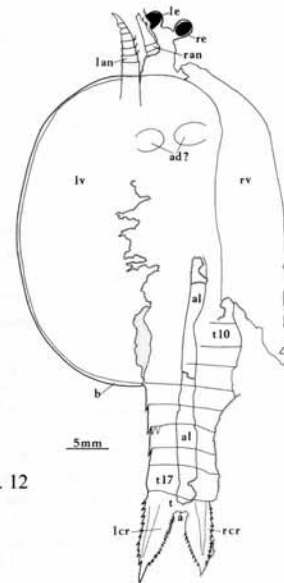
The telson was suboval in cross-section as the height is greater in lateral (Pl. 67, figs. 1, 2) than the width in parallel aspect (Pl. 68, fig. 4). The furcal rami are similar in dimension in both lateral (Pl. 67, figs. 1, 2) and parallel specimens (Pl. 67, fig. 7). The dorsal and outer margins were slightly concave, the ventral and inner more markedly convex (Pl. 67, figs. 1, 2; Pl. 69, fig. 1), the rami tapering to a point distally. Each ramus bore four symmetrically arranged rows of short, posteriorly directed spines, one pair in a vertical plane, the other transverse. One pair is usually preserved in outline, the vertical in lateral aspect (Pl. 67, figs. 1-5), the transverse in parallel (Pl. 69, fig. 1), as it is compressed into the plane of bedding. One of the rows normal to the plane of bedding is preserved as a series of ridges or grooves (Pl. 68, figs. 5, 7) depending upon which side of the part or counterpart it remains; the other may appear in relief, compressed through the cuticle from the reverse side (the left ramus of USNM 189245, Pl. 68, fig. 7). The dorsal, ventral (Pl. 67, figs. 1, 2), and outer rows included up to twelve evenly distributed, stout spines, the inner row up to sixteen finer and more closely spaced (Pl. 68, figs. 5, 7). The anus was situated mid-ventrally on a slight projection flanked by a spinose caudal furca (Pl. 67, figs. 1, 2; Pl. 69, fig. 1). The furcal rami diverged to varying degrees (cf. Pl. 68, fig. 4 and Pl. 69, fig. 1) but there is no evidence to confirm that they articulated with the telson.

Evidence of the alimentary canal is preserved in seven of the eleven specimens. This may consist of a relief trace, due to an original sediment fill (Pl. 68, fig. 4; Pl. 69, fig. 1), or a reflective strip (Pl. 67, fig. 8). Where both types of preservation occur on a single specimen (Pl. 67, figs. 1, 2) the width of the reflective trace may be variable, and considerably less than that preserved in relief; it may not reliably represent the original. The relief trace occupies up to one-third of the width of the trunk somites just posterior of the carapace (Pl. 67, figs. 1, 2; Pl. 68, fig. 4). The alimentary canal was presumably subcircular in cross-section, as the sediment-filled outline is similar in both lateral (Pl. 67, fig. 2) and parallel (Pl. 68, fig. 4) aspect. It was situated mid-ventrally, at least in those somites which extended posteriorly beyond the carapace. Traces of the alimentary canal extend anteriorly into the thoracic somites (Pl. 67, figs. 1, 2; Pl. 69, figs. 1, 2). No evidence of gut diverticula has been observed. The darker colour of the sediment fill on USNM 213804 (Pl. 69, figs. 1, 2), relative to the surrounding cuticle, may be due to the gut contents.

Thoracic appendages. Evidence for the arrangement and character of the appendages is slight due to inadequate preservation and the small size of the specimens. Removal of the right valve of USNM 189280 (Pl. 67, figs. 3, 4), has revealed evidence of the presence of ten poorly preserved appendages. These appear to have been large, flattened, lamellate, suboval features, overlapping posteriorly. Evidence of flattened



TEXT-FIG. 11



TEXT-FIG. 12

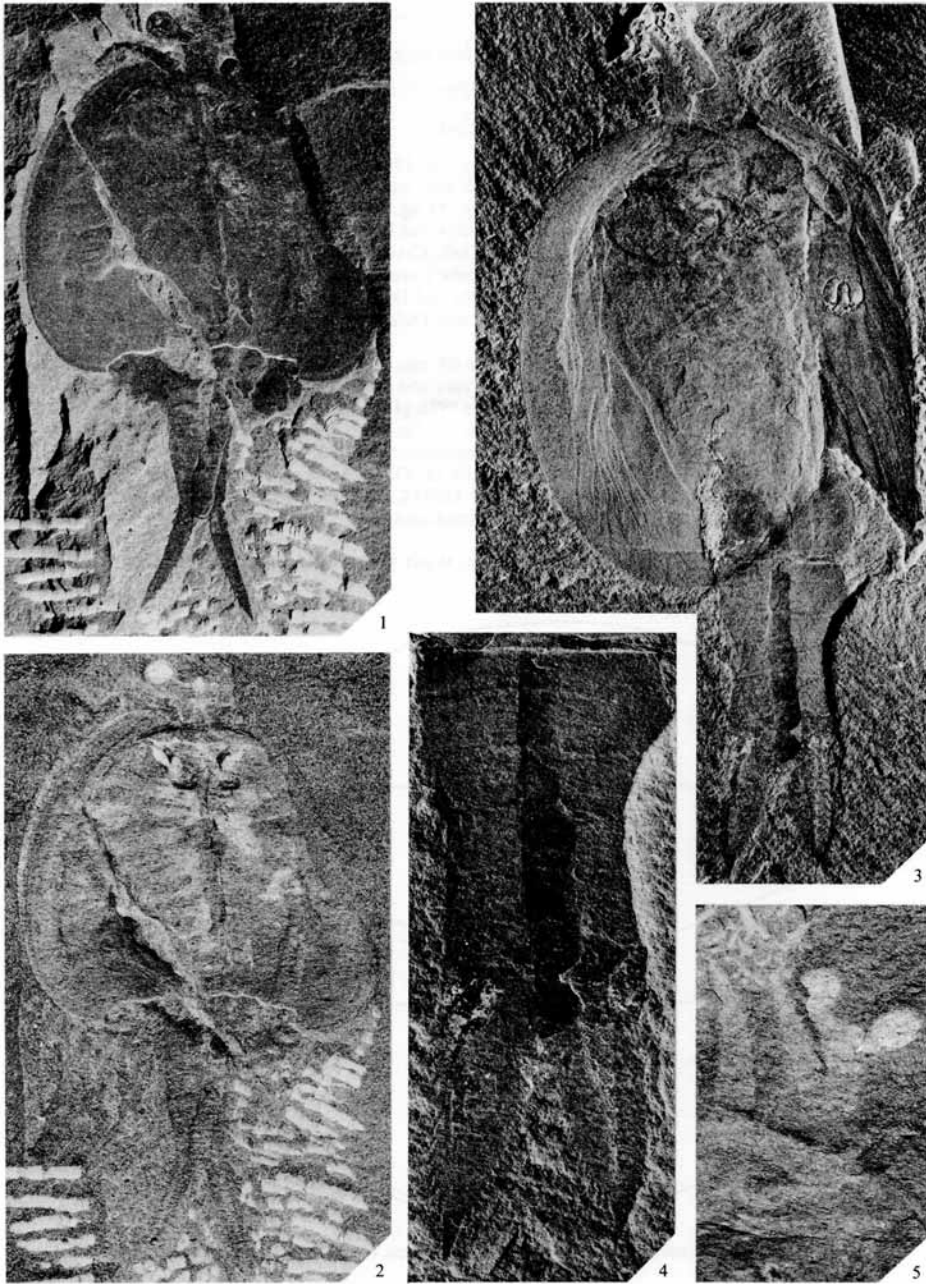
appendages is also preserved in parallel (Pl. 69, fig. 1) and oblique aspect (Pl. 68, fig. 7). There is no unequivocal evidence that they were biramous. Very tenuous reflective and relief traces on the appendages of USNM 213804 (Pl. 69, figs. 1, 2) may represent the outline and claws of an ambulatory ramus, but these have proved impossible to photograph. Ventral corrugations corresponding to the reflective bands on the thorax of USNM 114244 (Pl. 67, figs. 1, 2) may also represent this postulated segmented ramus. The thoracic appendages are not reconstructed in detail (text-fig. 1).

Size. Both the flexibility of the trunk and the flattening of the carapace in several orientations, allied to its incompleteness in some specimens, impose limitations on the accuracy of an assessment of the size range. Values for the maximum length of the carapace parallel to the hinge line (l) and the total sagittal length (L) from the anterior margin of the carapace to the distal extremity of the caudal furca are as follows: mean $l = 11.33$ mm, variance = 6.32, $N = 9$; mean $L = 22.4$ mm, variance = 21.79, $N = 7$. The fraction of the total length (L) occupied by the carapace (l): mean = 0.54, variance = 0.0021, $N = 7$. The size ranges between USNM 207245 (Pl. 68, figs. 1, 2), $l = 7.5$ mm, and USNM 213804 (Pl. 69, figs. 1, 2), $l = 16.5$ mm, $L = 29.0$ mm. The relative dimensions of the carapace are most satisfactorily shown by USNM 114244 (Pl. 67, figs. 1, 2); it is 11.6 mm long and 5.2 mm high normal to the hinge (these figures can not allow for the original convexity). The hinge line is too poorly preserved anteriorly to permit measurement.

EXPLANATION OF PLATE 69

Figs. 1, 2. *Perspicaris dictynna* (Simonetta and Delle Cave, 1975). USNM 213804, parallel, ventral aspect: 1, north-west, $\times 3$; 2, north, reflected, $\times 3$; text-fig. 11.

Figs. 3-5. *Perspicaris recondita* gen. et sp. nov. USNM 114255, parallel-oblique: 3, west, $\times 2$; 4, north-east, $\times 4$, showing posterior trunk somites and telson; 5, north, reflected, $\times 4$, showing eyes and antennae; original of Simonetta and Delle Cave 1975, pl. 53, fig. 6; text-fig. 12.



BRIGGS, *Perspicaris* from the Burgess Shale

Perspicaris recondita gen. et sp. nov.

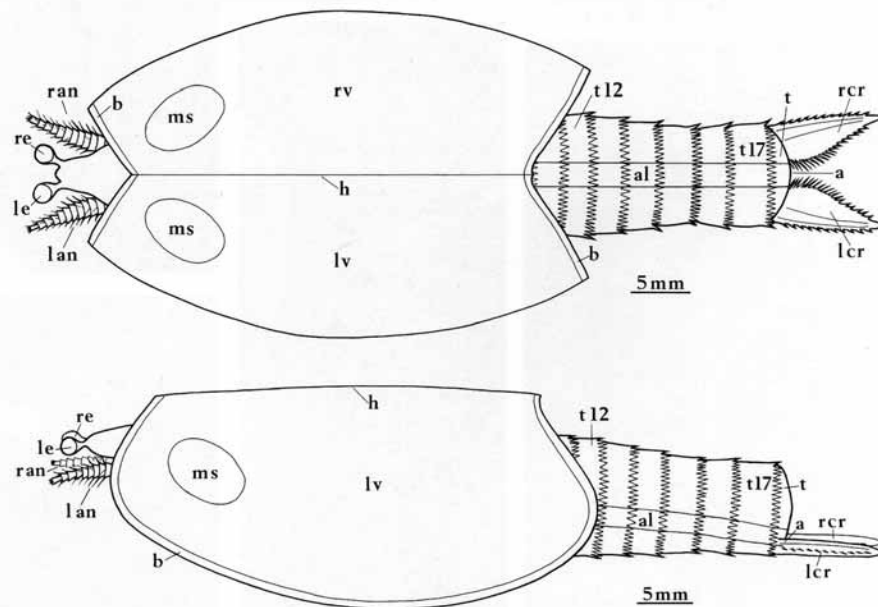
Plate 69, figs. 3-5; Plates 70, 71; Plate 72, figs. 1-7; text-figs. 12-24

Derivation of species name. Latin: recondita (concealed).

- 1912 *Hymenocaris perfecta* Walcott *pars*, pp. 152-153, 183-185, 222, pl. 31, figs. 2, 4.
 1929 *Hymenocaris perfecta* Walcott; Gürich *pars*, pp. 41, 42.
 1929 '*Hymenocaris*' *perfecta*; Gürich *pars*, p. 39, fig. 2, no. 1a.
 1975 *Canadaspis perfecta* (Walcott); Simonetta and Delle Cave *pars*, pl. 38, fig. 6.
 1975 *Canadaspis* cf. *obesa* Simonetta and Delle Cave *pars*, pl. 39, figs. 9, 10.
 1975 *Canadaspis dictynna* Simonetta and Delle Cave *pars*, p. 12, pl. 39, fig. 11.
 1975 ?*Carnavonia venosa* Walcott; Simonetta and Delle Cave *pars*, p. 13, pl. 36, fig. 2.
 1975 *Protocaris pretiosa* Resser; Simonetta and Delle Cave *pars*, p. 13, pl. 53, figs. 5, 6.

Holotype. USNM 114255 (designated herein), Plate 69, figs. 3-5, original of Simonetta and Delle Cave 1975, pl. 53, fig. 6. *Other material.* USNM 57704 part and SM A1709 counterpart, former original of Walcott 1912, pl. 31, fig. 2; Simonetta and Delle Cave 1975, pl. 38, fig. 6. USNM 57706, original of Walcott 1912, pl. 31, fig. 4; line drawing of Gürich 1929, pl. 39, fig. 2, no. 1a; Simonetta and Delle Cave 1975, pl. 39, fig. 9, and counterpart. USNM 114245 with counterpart, 189172, 189240 with counterpart, originals of Simonetta and Delle Cave 1975, pl. 39, figs. 11, 10, pl. 53, fig. 5 respectively. USNM 207312, 207313, GSC 45280 with counterpart, ROM 34305. USNM 189244, original of Simonetta and Delle Cave 1975, pl. 36, fig. 2, and 207314, with counterparts, are isolated carapaces.

Diagnosis. Furcal rami flattened, leaf like, with spinose lateral margins and median ridge.



TEXT-FIGS. 13, 14. Reconstructions of *Perspicaris recondita* gen. et sp. nov. 13, dorsal view. 14, lateral view.

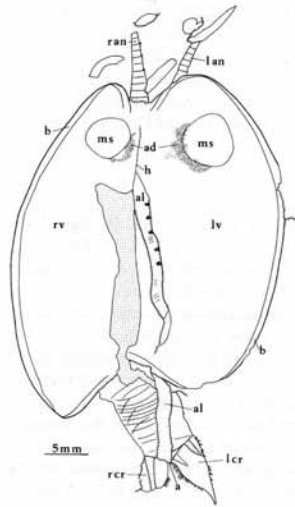
Locality and stratigraphical horizon. The USNM specimens bear the locality number 35k, except for USNM 114255 and 207313 which are not labelled, but all were presumably collected from the 'Phyllopod bed' in the Walcott Quarry. The single identifiable specimen collected by the GSC expeditions (Whittington 1971) came from the level 7 ft 4 in. to 7 ft 8 in. which also yielded abundant specimens of *Canadaspis perfecta*, several of which are also present on the slab. All the USNM specimens of *Perspicaris recondita* are on small pieces with only an incomplete agnostid and unidentifiable fragments in association, which do not indicate their level in the quarry.

DESCRIPTION

Cephalic region. The cephalon bore a pair of pedunculate eyes and elongate antennae (Pl. 69, figs. 3, 5) similar to those of *P. dictynna*. Removal of the carapace anteriorly from USNM 189240 (Pl. 71, figs. 4, 6), revealed an irregular amorphous area proximal of the antennae which may represent part of the cephalic region. This area is discontinuous laterally and posteriorly, presumably due to the effects of decay.

The eyes were borne at the antero-lateral corners of a distally tapering projection of the cephalon, wider than that in *P. dictynna*, which terminated in a gently convex anterior margin (Pl. 69, figs. 3, 5; Pl. 71, fig. 2). There is no evidence that this projection was segmented, but a degree of flexibility is indicated by a slight inclination to the right and hence dorsally on USNM 114255 (Pl. 69, fig. 3) and in the same direction, and therefore ventrally, on GSC 45280 (Pl. 71, fig. 1), but this may be an effect of orientation. The outline of the eyes and the stalk upon which they were borne can not be deduced in cross-section in the absence of a specimen preserved in lateral aspect, but is assumed to have been subcircular for the purposes of reconstruction (text-figs. 13, 14). The antennae included at least sixteen segments which are evident on the right antenna of USNM 189240 (combining the evidence of part and counterpart, Pl. 71, figs. 6, 7). A group of small, closely spaced spines, revealed by the removal of the carapace overlying the cephalic region on the part of USNM 189240 (Pl. 71, fig. 6), may have projected laterally from a proximal segment. The antenna appears to have terminated in several small spines (Pl. 71, fig. 7), and was clearly flexible. Removal of part of the carapace of GSC 45280 (Pl. 71, fig. 3; text-fig. 19) revealed the presence of a small projection or appendage emerging laterally from beneath the proximal segments of the right antenna. The nature of this projection is unknown, but it appears to have been divided into at least seven short, wide segments which extended laterally into small, blunt processes, and it may represent a second antenna. It is omitted from the reconstruction (text-fig. 14). The maximum known anterior extension of the alimentary canal is preserved on USNM 57704/SM A1709 (Pl. 70, figs. 1, 2) but the trace terminates at a point posterior of the cephalic region. A small, spinose appendage which projects anteriorly from beneath the right valve of USNM 207312 (Pl. 72, figs. 1, 3) may be cephalic. The distal extremity bore a series of closely spaced, fine, elongate, ventrally curved spines along the ventral margin. The dorsal margin was smooth and appears to be gently curved, convex dorsally. The proximal outline of the appendage, exposed by a removal of the overlying valve, is poorly defined, and the limb may not be *in situ*. It is not included in the reconstruction (text-figs. 13, 14) for this reason.

Carapace. The carapace was similar in outline and attachment to that of *P. dictynna*. The muscle scars are likewise flanked on some specimens by dark reflective features which may represent traces of the adductor muscles (Pl. 70, figs. 1, 2; Pl. 71, fig. 2). Two small, adjacent oval features preserved posterior of the cephalic appendages of USNM 114255 (Pl. 69, fig. 3) may represent the attachment of the adductor muscles to the cephalon. The hinge line is slightly convex dorsally in lateral aspect on USNM 207312 (Pl. 72, fig. 3), but this may be an effect of compaction. Its posterior extremity was produced into a small, blunt triangular area (Pl. 72, fig. 3; Pl. 71, figs. 4, 5). The hinge line is obscured anteriorly on the specimens preserved in parallel (Pl. 70, figs. 1, 2) and parallel-oblique aspect (Pl. 69, fig. 3; Pl. 71, figs. 1, 4, 5) but there is no evidence that it was similarly produced in this direction. Both the anterior and posterior margins of the valve diverged from the hinge at angles of 120°–130° (Pl. 72, fig. 3; Pl. 70, figs. 1, 2), but the posterior embayment of the carapace was deeper than the anterior due to the extension of the valves postero-ventrally. The valves are assumed to have been joined by a band of flexible cuticle, such as that postulated for *P. dictynna*. An indication of the original convexity of the carapace is provided by the closely spaced concentric folds around the ventral margins of the valves of USNM 57704/SM A1709 (Pl. 70, figs. 1, 2), for example. The carapace is usually smooth apart from such folds and wrinkles, the adductor muscle scars, and a border which sloped slightly abaxially and was bounded on its inner margin by a shallow groove (Pl. 70, figs. 1, 2; Pl. 71, figs. 1, 4, 5). The border was covered in a vermicular pattern of short,



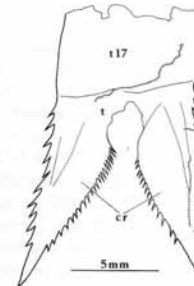
TEXT-FIG. 15



TEXT-FIG. 17



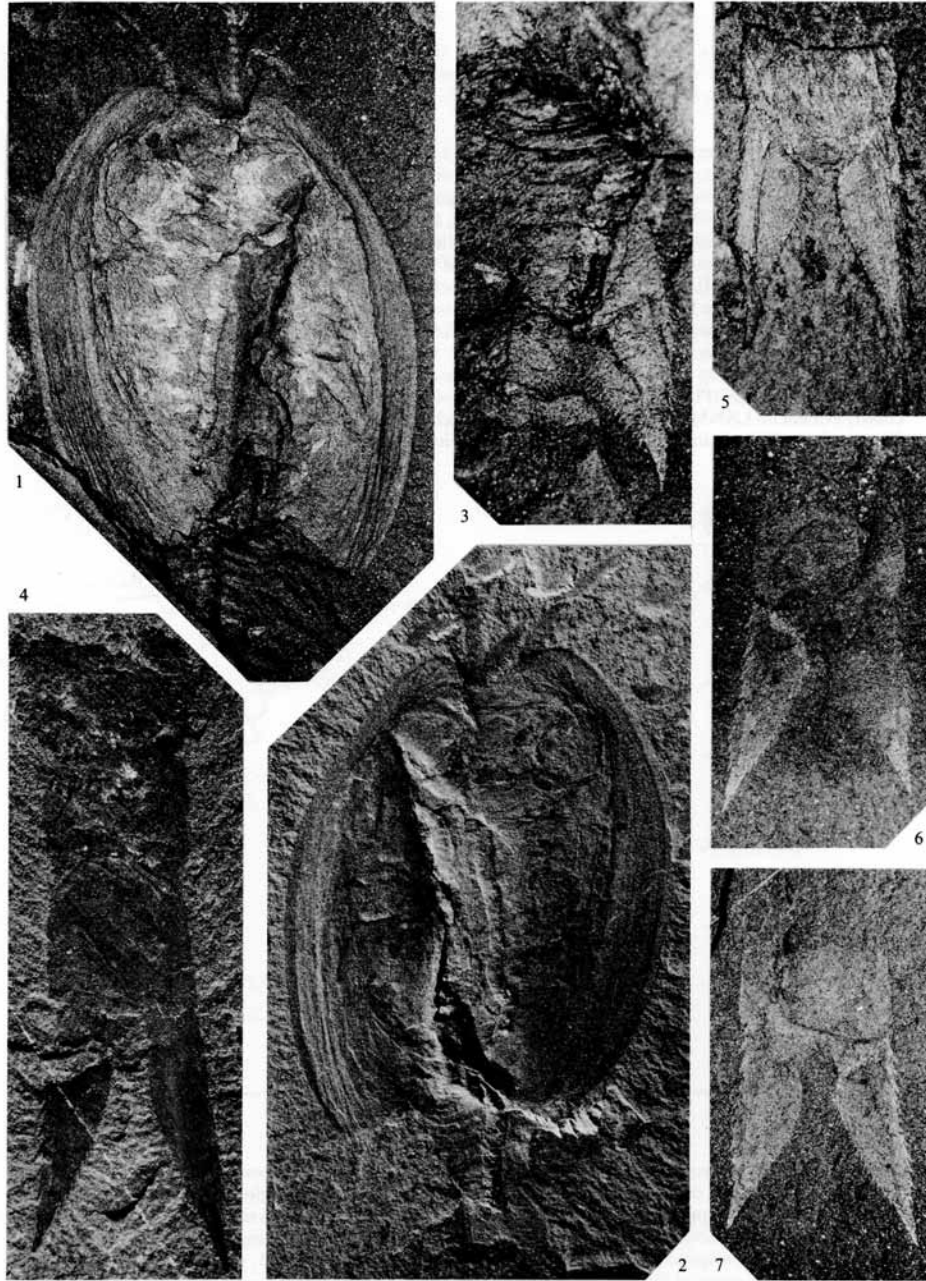
TEXT-FIG. 16



TEXT-FIG. 18

EXPLANATION OF PLATE 70

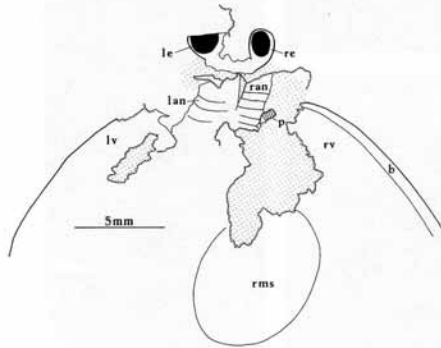
Figs. 1-7. *Perspicaris recondita* gen. et sp. nov. 1-3, USNM 57704, part, and SM A1709, counterpart, parallel: 1, USNM 57704, east, reflected, $\times 2$, original of Walcott 1912, pl. 31, fig. 2, Simonetta and Delle Cave 1975, pl. 38, fig. 6; 2, 3, SM A1709: 2, north-east, $\times 2$; 3, south, reflected, $\times 4$, showing telson; text-fig. 15. 4, USNM 114245, parallel, north, $\times 4$, original of Simonetta and Delle Cave 1975, pl. 39, fig. 11b; text-fig. 16. 5, USNM 189172, parallel, north, reflected, $\times 3$, original of Simonetta and Delle Cave 1975, pl. 39, fig. 10; text-fig. 17. 6, 7, USNM 57706, part and counterpart, parallel: 6, south, reflected, $\times 3$, original of Walcott 1912, pl. 31, fig. 4, Simonetta and Delle Cave 1975, pl. 39, fig. 9; 7, east, reflected, $\times 3$; text-fig. 18.



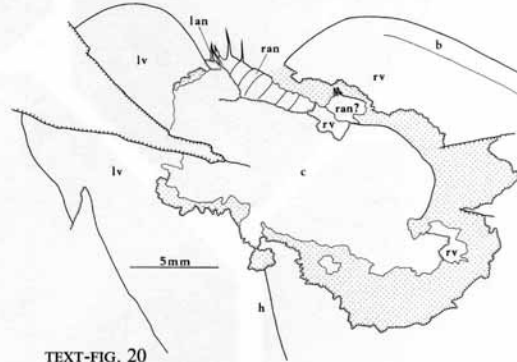
BRIGGS, *Perspicaris* from the Burgess Shale

closely spaced, elongate ridges orientated parallel to the margin (Pl. 72, fig. 5), which may be virtually invisible depending on the nature of the preservation. A reticulate pattern occurs on the carapace of USNM 207312 (Pl. 72, figs. 3, 4) and 189244 (Pl. 72, fig. 7), but is absent on the other specimens (see Discussion).

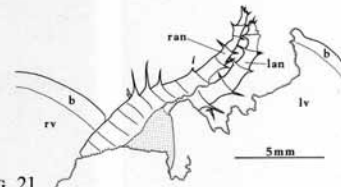
Trunk. The anterior somites of the trunk are obscured by the overlying carapace, and even where the latter is partly lacking due to exfoliation or fortuitous splitting of the fossil (Pl. 69, fig. 3) no evidence of their morphology has been observed. A series of highly reflective areas preserved on the trace of the alimentary canal on the part of USNM 57704/SM A1709 (Pl. 70, fig. 1) may reflect the arrangement of the adjacent somites, but they can not be accurately enumerated. Nine posterior somites are evident on USNM 207312 (Pl. 72, fig. 2) in addition to the telson, seven on USNM 114245 (Pl. 70, fig. 4), and at least eight on USNM 114255 (Pl. 69, figs. 3, 4). The trunk somites are numbered assuming a total of seventeen as in *P. dictynna* (text-figs. 13, 14). All the known examples of the posterior trunk somites and telson are preserved in parallel aspect. The trunk diminished gradually in width posteriorly to the anterior margin of the pre-telson somite, which was slightly wider than that preceding it (Pl. 72, fig. 2; Pl. 70, fig. 4). The posterior margin of each somite was fringed by up to fifty, closely spaced, elongate spines (Pl. 70, fig. 4). The inter-somite boundaries are preserved in relief (Pl. 69, fig. 4) due to an overlap of the cuticle of successive somites, and this is particularly evident on USNM 207312 (Pl. 72, figs. 2, 3), which preserves the cuticle of both sides of the abdomen. The trunk was presumably flexible, although there is little evidence to support this contention apart from



TEXT-FIG. 19



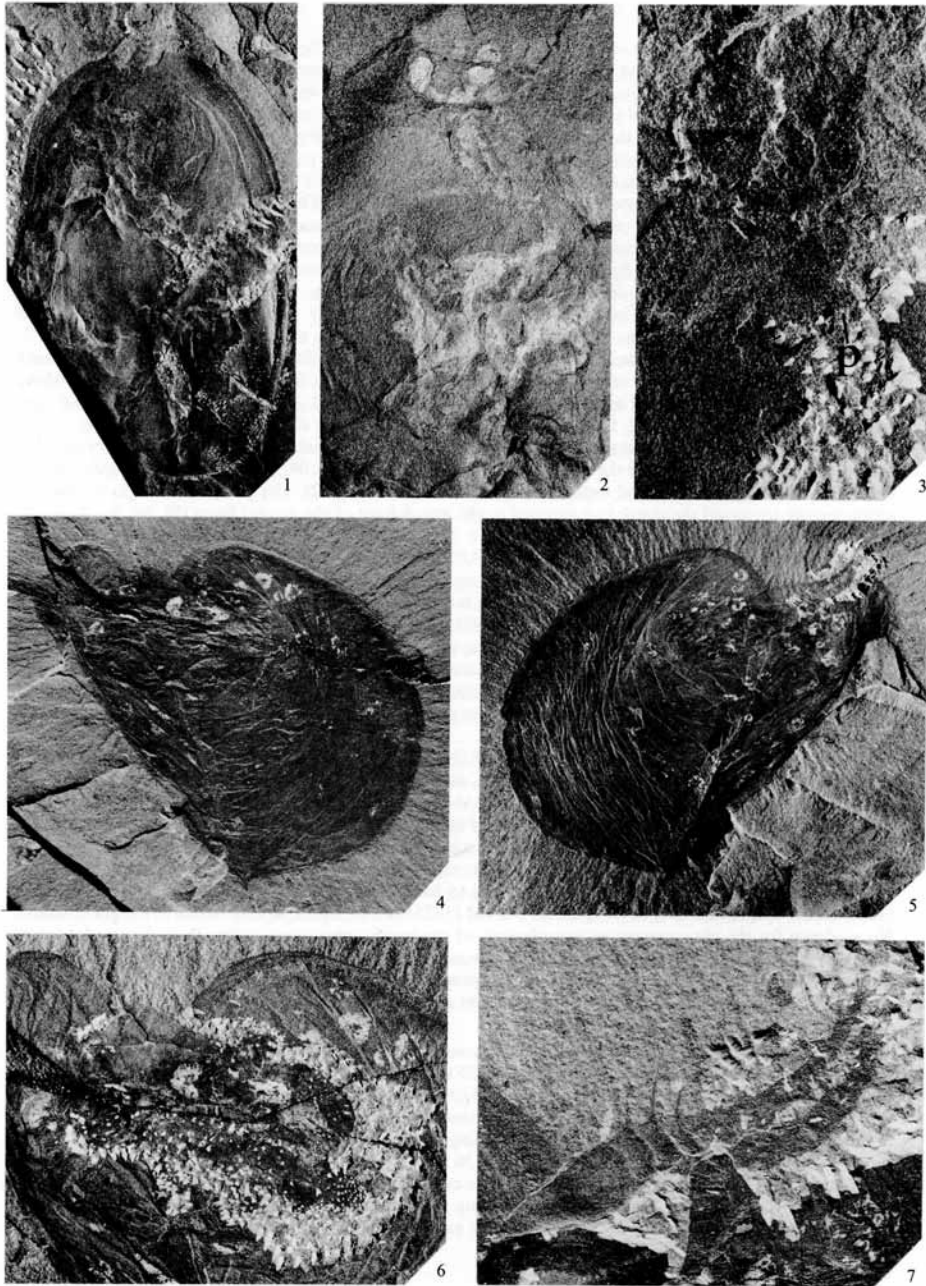
TEXT-FIG. 20



TEXT-FIG. 21

EXPLANATION OF PLATE 71

Figs. 1-7. *Perspicaris recondita* gen. et sp. nov. 1-3. GSC 45280, part and counterpart, parallel-oblique: 1, part, east, $\times 1.5$; 2, counterpart, east, reflected, $\times 3$, showing cephalic region; 3, part, west, $\times 6$, showing eyes, and small appendage? ventral of right antenna revealed by removal of carapace in this area; text-fig. 19. 4-7, USNM 189240, part and counterpart, oblique: 4, part, north, $\times 1.5$; 5, counterpart, north-east, $\times 1.5$, original of Simonetta and Delle Cave 1975, pl. 53, fig. 5; 6, part, east, $\times 3$, showing cephalic? region revealed by removal of part of carapace; 7, counterpart, north, $\times 6$, showing antennae revealed by removal of anterior margin of left valve; text-figs. 20, 21.



BRIGGS, *Perspicaris* from the Burgess Shale

the configuration of the somites of USNM 57704/SM A1709 (Pl. 70, figs. 2, 3) which appear to have been compacted at a high angle to the carapace, possibly due to a pronounced ventral curvature. The sagittal length of successive somites appears to have decreased slightly anteriorly (Pl. 72, fig. 2; Pl. 69, fig. 4) as in *P. dictynna*. The cross-section is assumed to have been subcircular (text-figs. 13, 14).

The telson was shorter than the preceding trunk somite, and bore a pair of broad, flattened, spinose furcal rami flanking the anus distally. Examples preserved in exactly parallel aspect (Pl. 69, fig. 4; Pl. 72, fig. 2) show that the outer margin of each ramus was slightly convex and the inner margin more strongly so, the ramus expanding rapidly posteriorly to a maximum width in about one-quarter the sagittal length, and tapering gradually distally to an elongate point. A slight obliquity of compaction may distort the outline or apparent width of the rami, the outer margin of one becoming slightly concave and that of the other almost straight (Pl. 70, figs. 6, 7; Pl. 72, fig. 6). Each ramus bore a series of posteriorly directed spines; up to eleven short, stout, and evenly spaced on the outer margin and over twenty, which became more elongate and closely spaced anteriorly, on the inner (Pl. 70, figs. 5-7; Pl. 72, figs. 2, 6). A ridge extended along the abaxial area of the ramus parallel to the outer margin and tapered towards the distal extremity (Pl. 72, fig. 2; Pl. 69, fig. 4). There is no evidence that this ridge was spinose. A similar feature is assumed to have been present on both the dorsal and ventral surface of the ramus although this is impossible to verify without a specimen preserved in lateral aspect. An indication of the original convexity is provided by the right ramus of USNM 207313 (Pl. 72, fig. 6), which has been flattened in a slightly oblique orientation.

The anus appears to have been situated slightly dorsal of the caudal furca. The alimentary canal is preserved in positive relief above the furcal rami on USNM 114255 (Pl. 69, figs. 3, 4), which affords a dorsal view, and below them, in ventral aspect, on SM A1709 (Pl. 70, fig. 2). The posterior margin of the pre-telson somite traversed the trunk just anterior to the attachment of the caudal furca (Pl. 69, fig. 4; Pl. 72, fig. 2). The telson was gently convex posteriorly (Pl. 72, fig. 2; Pl. 70, fig. 5), and extended over the attachment of the furcal rami (Pl. 69, fig. 4; Pl. 70, fig. 4). USNM 207312 (Pl. 72, fig. 2) appears to afford a ventral view of the telson; the caudal furca lies at the same level as the exposed (uppermost) side of the trunk, and the cuticle of the telson lying between the rami is at a lower level and thus apparently dorsal. A feature preserved between the furcal rami of USNM 114255 (Pl. 69, figs. 3, 4), extending ventrally beyond the trace of the alimentary canal, may represent cuticle which supported the anus. Evidence for the presence of an articulation at the base of the furcal rami is confined to an apparent thickening of the cuticle at this point (Pl. 72, fig. 2) which may extend anteriorly along the lateral margin of the pre-telson somite (Pl. 70, fig. 5). The expansion of this somite relative to those preceding it suggests that it may have accommodated muscles employed in movement of the furca.

The course of the alimentary canal anterior of the telson is evident on only two specimens, USNM 57704/SM A1709 (Pl. 70, figs. 1, 2) and 114255 (Pl. 69, figs. 3, 4), but in both cases it is preserved in relief, presumably due to a sediment fill. It follows the mid-line of the trunk in parallel aspect, occupying about one-sixth of the width of the somites just posterior of the carapace. The trace of the canal, although distorted, extends anteriorly almost as far as the carapace muscle scars on USNM 57704/SM A1709 (Pl. 70, figs. 1, 2), but there is no indication of its course in the cephalic region. No evidence for the presence of gut diverticula has been observed. The wall of the canal appears to have been annulated, but this may be a feature of preservation. The dark colour of the trace on USNM 114255 (Pl. 69, figs. 3, 4) may be due to the gut contents. No evidence for the arrangement or morphology of the trunk appendages (other than the caudal furca) has been revealed by detailed examination or preparation of the known specimens, apart from poorly preserved traces on ROM 34305, which may represent lamellate rami. Appendages do not, however, appear to have been borne by at least seven or eight somites anterior of the telson.

Size. The same considerations apply as to *P. dictynna*. Mean $l = 44.25$ mm, variance 34.92, $N = 4$. L can only be measured for two specimens: USNM 114255 (Pl. 69, fig. 3), $L = 57$ mm, $l/L = 0.63$; USNM 57704/SM A1709 (Pl. 70, figs. 1, 2), $L = 50$ mm, $l/L = 0.90$ (this value is disproportionately high due to the orientation of the posterior trunk somites during compaction). The remaining specimens are either distorted due to flattening in an oblique orientation to the bedding or too fragmentary to permit comparison. The size ranges between USNM 114255 (Pl. 69, fig. 3), $l = 36$ mm, $L = 57$ mm, and USNM 207312 (Pl. 72, fig. 3), $l = 50$ mm. The relative dimensions of the carapace can be most accurately measured on the right valve of USNM 207312 (Pl. 72, fig. 3), which is 50 mm long and 28 mm high (these values can not allow for the original convexity). The antero-dorsal apex of this valve is lacking, however, preventing measurement of the hinge line.

DISCUSSION

Previous descriptions. Walcott (1912, pl. 32, figs. 5, 6) described *Hymenocaris ovalis* on the basis of two specimens, USNM 57714 and 57715. Simonetta and Delle Cave (1975) identified USNM 57715 as *Canadaspis perfecta* (pl. 38, fig. 8) and designated USNM 57714, an isolated valve, as the lectotype of *C. ovalis*, reconstructing the species on the evidence of three additional specimens, USNM 114244 (Pl. 67, figs. 1, 2) 114254 (Pl. 68, fig. 4), and 189242 (Pl. 67, fig. 7). An isolated valve is not considered a reliable basis for a species due to the over-all similarity of the carapaces of *Canadaspis* and *Perspicaris*, for example, and the pronounced variation in outline caused by different orientations to the bedding. USNM 114244, 114254, and 189242 are therefore removed from *C. ovalis* (which is left occupied by the indeterminate lectotype alone) and referred to *C. dictynna* Simonetta and Delle Cave, 1975, as they are conspecific with the holotype of this species, USNM 189280 (Pl. 67, figs. 3-5). The second specimen referred by Simonetta and Delle Cave to *C. dictynna*, however (USNM 114245, pl. 39, fig. 11), differs in the morphology of the caudal furca, and is placed in *P. recondita*. Simonetta and Delle Cave's reconstructions of *C. dictynna* and *C. ovalis* (pl. 5, figs. 4 and 3 respectively) are thus largely based on individuals considered herein to belong to the same species of *Perspicaris*. There is little evidence to support either the occurrence of the thirteen pairs of elongate 'legs' depicted on their reconstruction of *C. ovalis* (pl. 5, fig. 3), or their contention (p. 12) that USNM 114254 (Pl. 68, fig. 4) indicates that 'probably the first two or three pairs of legs were somewhat specialized as mouth parts or as grasping organs' (cf. Pl. 67, fig. 4).

Walcott (1912) assigned USNM 57704 (Pl. 70, fig. 1) and 57706 (Pl. 70, figs. 6, 7), referred herein to *P. recondita*, to *Hymenocaris* (i.e. *Canadaspis perfecta*). He observed (1912, p. 183) that USNM 57704 'shows the antennae to be jointed', but added (p. 184), with reference to the same specimen, that 'they may, however, be straight, unjointed and long'. This confusion may have arisen as a result of traces of extraneous organic matter in the vicinity of the antennae (Pl. 70, fig. 2). Walcott (1912, p. 222) considered that USNM 57704 shows 'traces of the basal joints of the legs' but it is not clear from his figure (1912, pl. 31, fig. 2) to which features he was referring; the reflective areas which flank the alimentary canal (Pl. 70, fig. 1) provide little support for his contention. Walcott (1912, p. 184) stated that 'the terminal segment' of *H.* (= *Canadaspis perfecta*) has 'from 2 to 6 cercopods attached to it', and illustrated the former configuration by USNM 57706 (1912, pl. 31, fig. 4). The telson of *P. recondita* (USNM 57706, Pl. 70, figs. 6, 7), however, bore a true caudal furca, whereas the distal 'ventral projections' in *C. perfecta* extended from the pre-telson somite. These 'ventral projections' were also paired, but deeply divided into spines which Walcott erroneously interpreted as individual 'cercopods'. Several subsequent authors (Henriksen 1928; Gürich 1929; Størmer 1944) commented on this misconception, but failed to note the fundamental difference between the distal morphology of USNM 57706 (Pl. 70, figs. 6, 7) and the specimens of *C. perfecta* which Walcott also figured (1912, pl. 31, figs. 3, 5).

Simonetta and Delle Cave (1975) assigned USNM 57704 (pl. 38, fig. 6) to *C. perfecta*, but removed USNM 57706 (pl. 39, fig. 9) and referred it, together with USNM 189172 (pl. 39, fig. 10; Pl. 70, fig. 5), to *C. cfr. obesa*. Their species *C. obesa*, however, is

based mainly on USNM 189019 (cited as USNM 189258, pl. 39, fig. 1) which appears to be a specimen of *C. perfecta* with a poorly preserved telson. Four additional specimens identified herein as *P. recondita* were also figured by Simonetta and Delle Cave. USNM 114255 (pl. 53, fig. 6; Pl. 69, fig. 3) and 114245 (pl. 39, fig. 11; Pl. 70, fig. 4), which show the caudal furca, were assigned to *Protocaris pretiosa* and *C. dictynna* respectively; USNM 189240 (pl. 53, fig. 5; Pl. 71, figs. 4, 5) and 189244 (pl. 36, fig. 2; Pl. 72, fig. 7), preserving a combination of characteristic features including the vermicular carapace border, to *P. pretiosa* and *Carnarvonina venosa*.

Mode of life, functional morphology. The preservation of *Perspiscaris dictynna* is essentially similar to that of *Marrella splendens* (Whittington, 1971) and most other Burgess Shale arthropods, and suggests that it was benthic in habitat. The material of *P. recondita*, however, includes a higher proportion of fragmentary specimens, which may represent exuviae or the remains of dead individuals. The expanded furcal rami of this species (text-figs. 13, 14) are much larger than in *P. dictynna*, and strikingly similar to those of the Recent *Nebaliopsis* (cf. Rolfe 1969, p. 313, fig. 133, 1c) which Rolfe (1969, p. 308) considered 'made sustained swimming possible' and explained the wide distribution of this form. *P. recondita* may thus have been nectic; the few complete specimens could have been overtaken by a cloud of sediment while swimming near the sea bed.

The large pedunculate eyes of *Perspiscaris* (text-figs. 1, 2, 13, 14), borne on an apparently flexible projection of the cephalon, presumably ensured a wide field of view; the antennae appear to have been sensory rather than locomotory in function. The lack of evidence for the nature of the thoracic appendages prevents a satisfactory discussion of their functional morphology. Those of *P. dictynna*, however, appear to have included large, lamellate branches (they may have been biramous) which probably served in swimming, and may have induced an anteriorly directed current along the ventral surface of the trunk between the appendages which functioned in respiration and feeding. The apparent flexibility of the trunk of *P. dictynna*, together with the arrangement of the spines on the caudal furca (text-figs. 1, 2), suggest that it may have employed a grooming action similar to that described by Sanders (1963, p. 13) in *Hutchinsoniella*—'the head appendages are cleaned by jack-knifing or doubling the abdomen under the thorax and cephalon and drawing the abdomen posteriorly through the head and trunk appendages to its normal position'. The spines on the furcal rami of *P. dictynna* may have functioned like the combs on the last abdominal somite and telson of *Hutchinsoniella*, which pass through the setae and spines of the appendages.

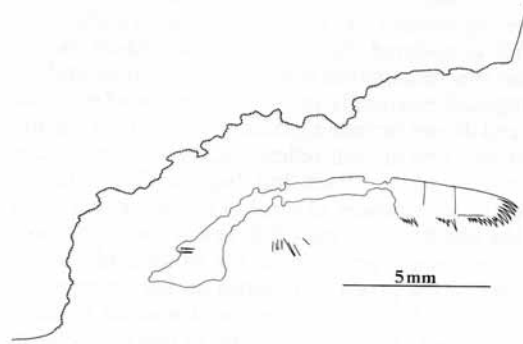
Carapace reticulation in P. recondita. A reticulate pattern covers the greater part of the valves of USNM 207312 and 189244 (Pl. 72, figs. 3, 4, 7) but has not been observed on the other specimens. The pattern is made up of irregular, rectilinear, polygonal areas (Pl. 72, fig. 4), which range in maximum width from 0.1 to 1.0 mm, but average from 0.3 to 0.5 mm. They are bounded on five, six, or seven sides by bands of darker material about 0.04 mm wide which are preserved in positive relief relative to the areas they enclose. The boundaries become ill-defined and less pronounced in relief towards the periphery of the reticulated area and appear to be obscured by an overlying layer of cuticle. Rolfe (1962*b*, p. 4) described a similar reticulate pattern in

patchy areas on a few specimens of *Proboscicaris agnosta*, also from the Burgess Shale, and noted its occurrence on specimens of *Hurdia victoria*, *Tuzoia*, and *Carnarvonina* from the same fauna. He considered, however, that the cuticle 'is too poorly preserved to ascertain whether this reticulation is sculptural or structural'.

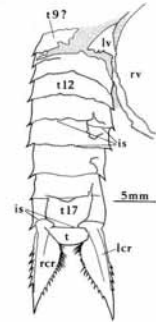
The Burgess Shale fossils are composed essentially of silicate minerals (personal communication S. Conway Morris) and do not include significant amounts of calcite. It is possible, however, that the carapace reticulation reflects the original prismatic structure of the cuticle of *Perspicaris recondita* which has been replaced during preservation. The variation in size and irregular shape of some of the polygonal areas on USNM 207312 (Pl. 72, fig. 4), the smallest of which fall well within the range observed by Rolfe (1962a, p. 45) on *Ceratiocaris papilio* from the Middle Silurian of Scotland, may be due to fusion of some of the prism boundaries during the replacement process. Some of the large, irregularly shaped polygons are traversed by faint traces which may represent original divisions. The concentration of fine reticulation along the longitudinal fold which accommodates the original convexity of flattened valves of *Tuzoia* (Resser 1929, pl. 1; pl. 2, fig. 1; pl. 3, figs. 1, 3) may be a reflection of some effect on the processes of preservation or diagenesis associated with the buckling of the carapace in this region. The specimens of *P. recondita* which show the reticulate pattern have been oxidized to a brownish-red colour, in contrast to the dark shiny material characteristic of the more finely preserved Burgess Shale fossils, and this 'weathering' process may have resulted in differential corrosion similar to that achieved by Rolfe (1962a) by controlled etching of *Ceratiocaris*. Visible evidence of the pattern may, on the other hand, be a function of the level through which the carapace has split.

A study of the carapace of the abundant *Canadaspis perfecta* using the scanning electron microscope revealed no evidence of primary microstructures, and it is unlikely that finer details of the cuticle of *P. recondita* are preserved. It is impossible to verify that the reticulate pattern on the carapace of *P. recondita* and other Burgess Shale arthropods is a reflection of the configuration of the organic matrix or prismatic structure of the cuticle but the evidence suggests that this may have been the case.

Affinities and classification. The largest known specimen of *P. dictynna* is less than half the size of the smallest of *P. recondita*. The difference in the caudal furca of the two species, however, and the lack of reticulation on the carapace of all examples of *P. dictynna*, suggest that it is unlikely to represent a juvenile of *P. recondita*. The two may, however, be sexual dimorphs. Rolfe (1969, p. 305) recorded that 'all Recent Leptostraca, except *Nebaliopsis*, show pronounced sexual dimorphism. . . . The carapace of the male is less deep than that of the female and the antennae are much larger. . . . The furca of the male *Nebalia* is also longer than that of the female.' *P. dictynna* might therefore, by analogy with the Leptostraca, be interpreted as the male dimorph, and *P. recondita* as the female. Some characteristics of sexual dimorphism in the Leptostraca do not, however, bear out the analogy. Males occur much more rarely than females, whereas the two species of *Perspicaris* occur in equal numbers. The longer antennae of the male Leptostraca are usually modified 'presumably to function as clasping organs' (Rolfe 1969, p. 306). There is no evidence of such specialization in the known appendages of *Perspicaris*. Glaessner (1931)



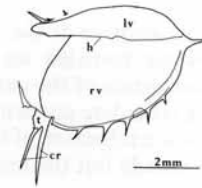
TEXT-FIG. 22



TEXT-FIG. 23



TEXT-FIG. 24

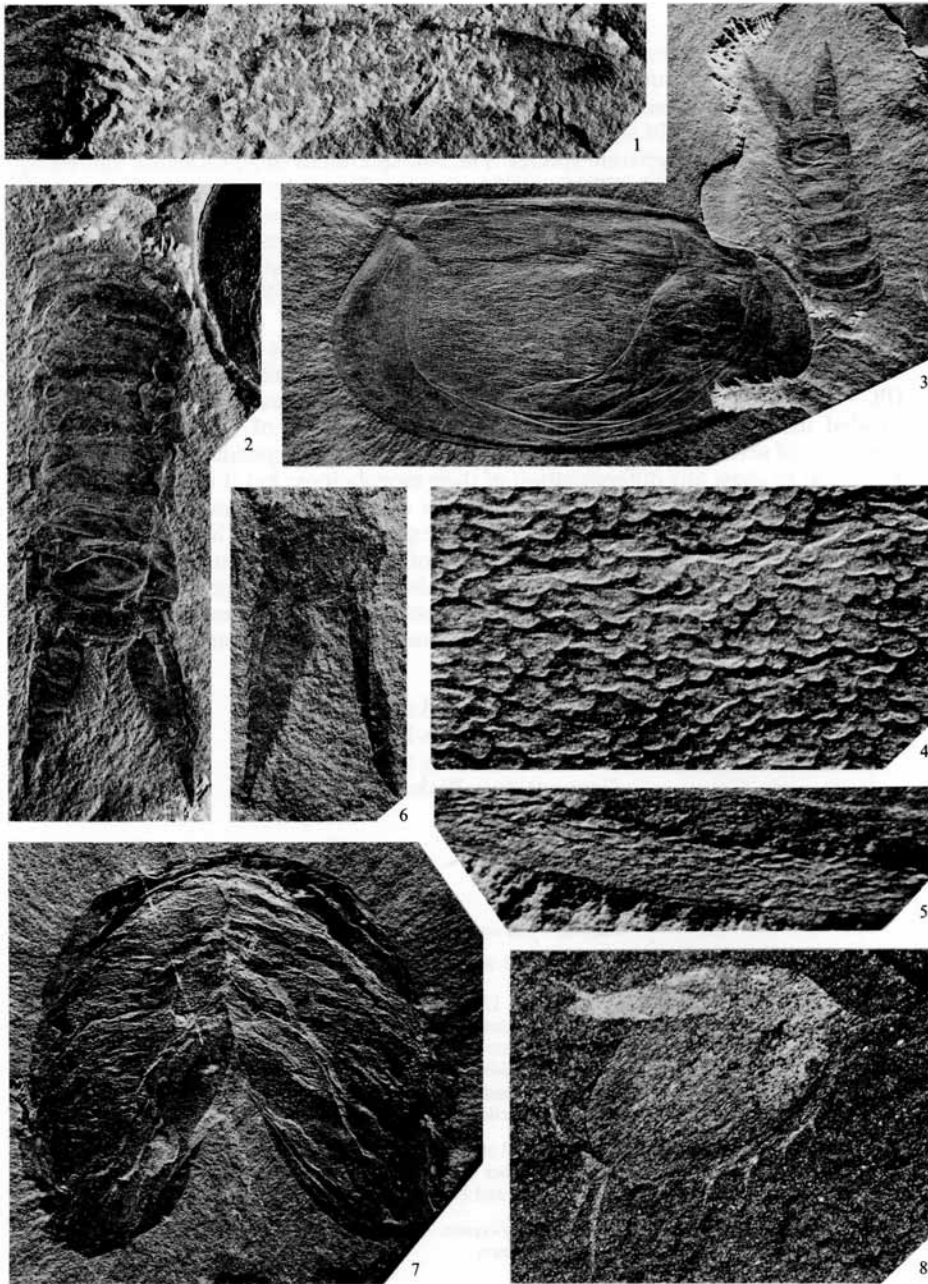


TEXT-FIG. 25

EXPLANATION OF PLATE 72

Figs. 1-7. *Perspicaris recondita* gen. et sp. nov. 1-5. USNM 207312, carapace lateral, trunk parallel. 1, west, $\times 6$, after preparation to reveal appendage at antero-ventral margin of carapace; 2, north-west, $\times 3$, showing posterior trunk somites and telson; 3, north, $\times 1.5$; 4, north, microscope, $\times 12$, showing reticulate pattern in central area of right valve; 5, north, microscope, $\times 12$, showing border at postero-ventral margin of right valve; text-figs. 22, 23. 6, USNM 207313, parallel-oblique, north-east, $\times 3$; text-fig. 24. 7, USNM 189244, vertical-oblique, north, $\times 2$, original of Simonetta and Delle Cave 1975, pl. 36, fig. 2a.

Fig. 8. *Tuzoia? parva* (Walcott, 1912). USNM 57716, lateral-oblique, north, reflected, $\times 10$, original of Walcott 1912, pl. 32, fig. 7, Simonetta and Delle Cave 1975, pl. 40, fig. 8; text-fig. 25.



BRIGGS, *Perspicaris* and *Tuzoia?* from the Burgess Shale

considered that variation in the carapace of one species of *Austriocaris* was due to sexual dimorphism, but the phenomenon has not been recorded in other fossil phyllocarids. In the absence of specimens of the early instars of the two 'forms' of *Perspiscaris*, which might show a convergence of morphology if they were dimorphs, they are described as separate species. The two specimens of *P. recondita* figured by Walcott (1912; USNM 57704, 57706) were referred by him to *Hymenocaris* (= *Canadaspis*) *perfecta*. *Perspiscaris* differs from *Canadaspis* in its larger eyes and antennae, and true caudal furca. The 'furca' of *Canadaspis* consists of a pair of spinose ventral projections of the seventh abdominal somite. *Perspiscaris* also differs from the type species of *Hymenocaris*, *H. vermicauda* Salter, 1853, in the nature of the carapace and telson (cf. Rolfe 1969, p. 315, fig. 135).

The morphology of *Perspiscaris* indicates strong affinities with the Phyllocarida. The evidence suggests that the cephalon of *P. recondita* bore two pairs of antennae (Pl. 71, fig. 3) and pedunculate eyes. The trunk of *P. dictynna* appears to have been divided into two tagmata, an appendage-bearing thorax of ten somites, and an abdomen of seven, in addition to the telson. The thoracic appendages are too poorly preserved to show any differentiation of their morphology, but it is possible that the anterior two pairs, although similar to those on successive somites, were cephalic (cf. *Hutchinsoniella* Sanders, 1963). Thus *Perspiscaris* may have had the division of somites diagnostic of the phyllocarids (see Rolfe 1969). The genus is referred to the Phyllocarida as the lack of a rostral plate and abdominal appendages is not considered sufficient to warrant the erection of a new subclass. A fuller discussion of the nature of the Phyllocarida in the light of new information on *C. perfecta* is in preparation.

Class MALACOSTRACA Latreille, 1806?
Subclass PHYLLOCARIDA Packard, 1879?
Order and Family uncertain
Genus TUZOIA Walcott, 1912?

Type species. *Tuzoia retifera* Walcott, 1912.

Geological horizon. As for *Perspiscaris*.

Tuzoia? parva (Walcott, 1912)

Plate 72, fig. 8; text-fig. 25

- 1912 ?*Hymenocaris parva* Walcott, pp. 153, 185, 224, pl. 32, fig. 7.
- 1925 ?*Hymenocaris parva* Walcott; Fedotov, pp. 386, 387.
- 1928 ?*Hymenocaris parva* Walcott; Henriksen, p. 14.
- 1929 *Hymenocaris (?) parva* Walcott; Gürich, p. 41.
- 1934 ?*Hymenocaris parva* Walcott; Straelen and Schmitz, pp. 34, 199, 211, 232.
- 1975 *Canadaspis* sp.; Simonetta and Delle Cave *pars*, pl. 40, fig. 8.

Holotype. USNM 57716, Plate 72, fig. 8, original of Walcott, 1912, pl. 32, fig. 7; Simonetta and Delle Cave 1975, pl. 40, fig. 8; by original designation. Other material unknown; Walcott (1912, p. 185) mentioned 'two specimens' but the second was not figured and has not been identified.

Locality and stratigraphical horizon. As for *P. dictynna*. The specimen bears the USNM locality number 35k, i.e. the 'Phyllopod bed' in the Walcott Quarry.

DESCRIPTION

The specimen (Pl. 72, fig. 8) is compacted in lateral-oblique aspect, the outline of the right valve apparently complete, the left folded beneath itself. The carapace appears to have been divided by a straight hinge line which was produced anteriorly into a long, straight spine or rostrum. The right valve is suboval in outline, tapering to a blunt anterior margin, and expanding postero-ventrally. The posterior margin is inclined to the hinge line at about 120° , creating a pronounced posterior embayment of the carapace. A break of slope parallel to the anterior margin may represent a fold accommodating the original convexity and suggests that this margin, which is inclined posteriorly at an angle of about 80° to the hinge, may have been foreshortened by compaction. The valve bore at least five elongate spines ventrally, directed posteriorly at an angle of 50° – 70° to the margin. The spinose features which project obliquely from beneath the posterior extremity of the left valve may also represent these spines. The dorsally directed 'spine' posterior of the right valve is preserved above the level of the carapace, and does not appear to be part of the specimen. The carapace appears to have been smooth apart from an indication of a narrow border preserved along the ventral margin of the right valve; no satisfactory evidence of a muscle scar has been observed. The small feature bearing a pair of long slender spines which projects ventrally from beneath the posterior margin of the right valve is considered to represent the telson and caudal furca, but no details of the morphology are preserved. The length of the right valve parallel to the hinge line, excluding the anterior spine, is 4.2 mm. The height normal to the hinge is 2.7 mm.

DISCUSSION

Previous descriptions. Walcott (1912, p. 185) offered a different interpretation of USNM 57716. He considered that the left valve was the abdomen which is 'pushed over on to the carapace' and that the furcal rami were 'the antennae' which 'project from the left side'. His figure (1912, pl. 32, fig. 7) appears to have been retouched to give a segmented appearance to the latter. Walcott interpreted the spines borne on the ventral margin of the right valve as appendages (p. 224). There is no evidence that the spines on the margin of the valve project from beneath it, as would be the case if they were appendages; they appear to be continuous with the border of the carapace. An interpretation of the relatively complete valve as the right-hand member of a pair is consistent with an anteriorly tapering outline, which occurs in many bivalved arthropods (e.g. *Perspikaris*, *Canadaspis*). The telson and caudal furca are thus in a position which they might be expected to occupy in a specimen preserved in the postulated orientation to the bedding. There is no evidence to support Walcott's contention that the folded left valve is part of the trunk.

Affinities and classification. Walcott (1912) tentatively referred USNM 57716 to *Hymenocaris* Salter, 1853 to which he also assigned specimens now described as *P. recondita* and *C. perfecta*. Subsequent authors (Fedotov 1925; Henriksen 1928; Gürich 1929; Straelen and Schmitz 1934) reiterated, but did not discuss, Walcott's doubt, which is clearly vindicated by the spinose margin of the carapace, a feature absent from *Hymenocaris*, *Canadaspis*, and *Perspikaris*. Simonetta and Delle Cave (1975), however, considered the specimen to be a juvenile of *Canadaspis* sp. indet. A spinose carapace occurs in the large bivalved genus *Tuzoia* Walcott, 1912, which is also present in the 'Phyllopod bed'. The generic assignment of *H.?* *parva* Walcott, 1912, remains equivocal. It is referred with a query to *Tuzoia*, to which it bears the greatest similarity, as there is insufficient evidence to warrant the erection of a new genus.

The valves of USNM 57716 appear to have tapered anteriorly, whereas Rolfe (1969, p. 327, fig. 152, no. 6) reconstructed that of *Tuzoia* expanding slightly in this direction. A comparison of Resser's two figured specimens of *T. burgessensis* (1929, pl. 2, fig. 1; pl. 3, fig. 1) suggests, however, that the valve may have tapered anteriorly, and that the outline of the specimen upon which Rolfe's reconstruction is based (USNM 80477, Resser 1929, pl. 2, fig. 1) has been altered by compaction. There is no evidence that the carapace of *T. ? parva* was reticulate, as is usually the case in *Tuzoia*, but this may be a feature of preservation; reticulation is not present, for example, on all specimens of *P. recondita*. *T. ? parva* also lacks the prominent ridge characteristic of the valves of *Tuzoia* (see Rolfe 1969, p. 328) which Resser (1929) referred to as a keel, but this feature varies in position (cf. Resser 1929, pl. 1, fig. 1 with pl. 1, fig. 2; pl. 2, fig. 1 with pl. 3, fig. 1, for example) and is probably due to compaction of the original convexity, which may have reached a maximum along the mid-line of the valve parallel to the hinge. *Tuzoia* bore spines on the posterior margin of the valves, and the posterior extremity of the hinge line was produced into a spine; these features appear to have been absent on *T. ? parva*.

T. ? parva may have been a juvenile or larval form of a larger bivalved arthropod. Juveniles of *C. perfecta* (with carapaces about 10 mm in length) do not appear to differ from the adults, but this may not have been the case in *T. ? parva*. The specimens of *Tuzoia* found at the Walcott Quarry vary from about 40 to 120 mm in length; smaller valves are unknown. Several authors (Henriksen 1928; Resser 1929) suggested that *Anomalocaris* Whiteaves, 1892 may have been the trunk of *Tuzoia*, but this genus is reinterpreted as the appendage of a large arthropod; the body of *Tuzoia* remains unknown. The bivalved carapace and apparently unsegmented caudal furca of *T. ? parva* support a tentative assignment to the subclass Phyllocarida.

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