Pygmaclypeatus daziensis, a unique lower Cambrian arthropod with two different compound eye systems

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More than half a billion years ago, a high diversity of organisms appeared in the fossil record. All major clades we know today already existed, and arthropods dominated the marine faunas. Many were already equipped with a pair of elaborated compound eyes on top of movable eye stalks. Some of them also possessed 3-4 small single-aperture eyes, so-called median eyes. Just trilobites possessed sessile dorsal eyes. One pair of compound eyes/lateral eyes is considered plesiomorphic and is a common trait for euarthropods. Here, we describe an arthropod that possessed two independent compound eye systems—a pair of stalked and a pair of tiny sessile dorsal trilobite-like compound eyes, unique in the arthropod kingdom so far. A competition between prey and predators for the capacity of vision triggered the evolution of visual systems, and we discuss this newly described system(s) in its evolutionary context and ecological significance. Regarding its eye system phylogenetically, *P. daziensis* reinforces the position of a now non-missing link between the non-trilobite artiopodans and trilobites.

To possess compound eyes is typical for most arthropods and a plesio-morphic character e.g., refs. [1–3]. Most early non-trilobite Cambrian arthropods possess stalked eyes comparable to modern crustaceans, for e.g., refs. [1,2], just trilobites are equipped with dorsal sessile compound eyes from their very appearance in the fossil record[3]. The race of arms between prey and predators of the Cambrian in the evolution of visual systems has been considered a trigger for the so-called Cambrian Explosion, the rapid radiation of metazoan diversity in the Early Cambrian during a short period of less than 25 million years, and determined the dynamics of these early ecological communities. Ferocious predators such as anomalocaridids and radiodonts possessed compound eyes with thousands of facets, which easily could have recognized their potential prey[4–6]. The smaller bottom dwellers, scavengers, and ground-feeding arthropods, on the other hand, were equipped with small, often light-sensitive, less acute movable stalk-eyes[1] that were aimed at detecting movement in a wide environment that enabled their bearers to escape as soon as possible. Meanwhile, the complexity of Cambrian eye systems and their implications have attracted the attention of many scientists, and overviews are given at refs. [1,7], and others.

Pygmaclypeatus daziensis[8] is among the less studied artiopodan, non-trilobite arthropods of the renowned early Cambrian Chengjiang biota of South China. While its ventral morphology was very recently unveiled[9], we have reinvestigated four specimens (Suppl. 1) and have discovered small dorsal sessile compound eyes and a pair of flexible, articulated stalked compound eyes anteriorly below the dorsal shield that had previously escaped analysis. Here, we analyze both visual systems by calculating specific physiological parameters[10–12]. Our analyses indicate that the dorsal compound eyes of *P. daziensis* were adapted to dim daylight conditions, suggesting that it inhabited shallow, probably slightly turbid waters. The ventrally oriented flexible stalked compound eyes under the headshield are more sensitive, scanning probably the ground for nutrients.

Pygmaclypeatus daziensis[8] and the context of artiopods in the Chengjiang Fauna

The Chengjiang biota of Cambrian Stage 3 in South China stands out globally as one of the most significant Konservat-Lagerstätten, primarily due to the pyritization process facilitating the fossilization of diverse non-

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biomineralizing organisms. Despite their pivotal role in elucidating early animals' evolution, numerous Chengjiang biota species remain poorly understood due to their rarity and/or incomplete preservation. One of those species is the non-trilobite artiopod *Pygmaclypeatus daziensis* [8], whose ventral and appendicular morphology was recently unveiled[9]. Within the Artiopoda[13], a diverse clade encompassing trilobites and related taxa with non-biomineralizing exoskeletons, *P. daziensis* stood out with a quite unique yet unknown appendicular morphology: a set of uniramous antennae and 14 pairs of post-antennal biramous appendages. Those appendages notably displayed a remarkable degree of heteronomy, characterized by localized differentiation of the protopodite, endopodite, and exopodite along the antero-posterior body axis. The head contained a set of four post-antennal biramous appendages, with the first three sharing a walking leg-like endopodite and a small and stenopodous exopodite. However, the fourth head appendages remained the walking leg-like endopodite, but featured a flap-like exopodite. The following trunk appendages then kept this flap-like exopodite, but shared a more robust and stout endopodite, which terminated in a subchelate structure, presumably used for grabbing and digging[9].

Pygmaclypeatus daziensis furthermore featured delicate spinose endites, which all together suggested an adaptation for a benthic or demersal lifestyle and presumably scavenging/detritus feeding strategy with its sharp terminal claws capable of piercing food items. However, no visual system has yet been discovered for *P. daziensis*, either ventrally or dorsally, which leads to the assumption that the organism lacks ocular structures. Among non-trilobite artiopodans and relatives from the Chengjiang biota, a variety of eye types were identified, some through state-of-the-art techniques like in-depth micro-CT examination and others through classical light microscopy in earlier studies (Table 1).

Results

The eyes found in these taxa were mostly rather large, conspicuous structures that either protruded from under the headshield anteriorly or antero-laterally, or their presence ventrally was inferred due to the fact that dorsal bulges or weak exoskeletal swellings were found dorsally. However, in *Pygmaclypeatus daziensis*, this was different. Here, no swellings or bulges indicating the presence of eyes were found dorsally in light microscopic analyses. The revealing micro-CT analyses also confirmed the assumption that this species lacked eyes ventrally.

However, only recently, upon re-examination of the previously analyzed *Pygmaclypeatus daziensis* specimens YKLP 11427 (Fig. 1a–c, Suppl.), and YKLP 13929 (Figs. 1e–i and 2a, b; Suppl. 1), we detected under light microscopic imaging techniques previously overlooked, tiny structures on the dorsal surface. Those herein will now be interpreted and explained as compound eyes. A third specimen has a distorted compound eye (YKLP 13928), Fig. 2a, b, j, k). In addition, we were also able to detect tiny articulated

stalked eyes (Fig. 2) that peeped out from under the dorsal shield or were hidden under it.

The functional structure of compound eyes and Synder's theory describe their performances.

One pair of compound eyes is considered plesiomorphic for euarthropods[7,14,15]. The oldest and most common type is the so-called apposition eye; more specialized types seem to have developed since the Carboniferous[16] but could well have evolved earlier. The apposition eye consists of numerous, sometimes up to 30,000 more or less identical units (*Anax* dragonflies[17]), from outside recognized as facets–the so-called ommatidia (Fig. 3a–d). Each ommatidium consists of a cuticular lens focusing the light through the cellular, transparent crystalline cone onto the tip of the light-guiding structure, the rhabdom. The rhabdom is part of the receptor cells and contains the visual pigments. With the energy of the incident light, these pigments change their steric configuration, producing an electrical signal that is passed by the nerves to the central nervous system for further processing. Because by focusing the rhabdom, all input signals, as contrasts for example, are summed up, each facet produces one pixel of an overall mosaic-like image generated by the compound eye in total. So, the acuity, among other factors, normally depends on the number of facets. In aquatic systems, however, often, the difference in optical density between water and the cuticular lens is not high enough for proper refracting, and the crystalline cone, formed as an index gradient lens, overtakes this function. These apposition eyes are typical for modern-day-active insects and crustaceans and could be described recently also for trilobites more than half a billion years old (*Schmidtiellus reetae*[18,19]).

$\Delta\varphi$ interommatidial angle, cc crystalline cone, pc pigment cell, r rhabdom, rc receptor cell. Copyrights were obtained for Fig. 3e, f (photographs),g.

In constructing a compound eye, there is always a conflict between the possible number of facets to achieve the highest possible acuity and the size of the lenses, which, under the given conditions, must capture sufficiently enough light. Because the amount of light available is the determining factor here, the resolution of this conflict provides reliable information about the lighting conditions in which an eye has been operating to ensure a functioning system. This applies to current as well as fossil systems.

Based on this basic idea, a theory to describe the performances of apposition compound eyes by their morphology was developed by the physicists Snyder, his colleagues[20–22], and Land[11] in the late 1970s, beginning 1980s, which was named later very aptly "*Optimum Compound Eye Design Theory*"[23,24]. This method of estimating the performance of eye systems using eye morphology has been successfully applied not only to recent systems, for e.g., refs. 11,25,26. but also to fossil ones[23,24,27].

To resolve two separate point objects in the environment, subtending an angle $\Delta\theta$ at the eye, three receptors are needed: one to detect each object and one to detect the space in between. The facets of a compound eye may be

Table 1 | Overview of eye system reports on Chengjiang arthropods

Taxon	Light microscopy	Microcomputer tomography
Acanthomeridion serratum[81]	- no evidence for eyes[13,81,85]	- in-depth micro-CT analyses are pending
Cindarella eucalla[54]	- large ventrally stalked eyes clearly preserved, protruding beyond the headshield[79,86–89]	-[90]
	- eyes on dorsally preserved fossils as weak exoskeletal swellings, putatively ventrally located[13,45,85–88,91]	- in-depth micro-CT analyses are pending
Saperion glumaceum[92]	- eyes on dorsally preserved fossils as weak exoskeletal swellings, putatively ventrally located[13,45,85–89,92]	- in-depth micro-CT analyses are pending
Sinoburius lunaris[13]	- presence of eyes speculated[13,85–89,92,93]	-[94,95] - ventrally located[95]
Skioldia aldna[14]	- eyes on dorsally preserved fossils as weak exoskeletal swellings, putatively ventrally located[13,85,88,96]	- in-depth micro-CT analyses are pending
Squamacula clypeata[14]	- no evidence for eyes[13,85,88,96–98]	- in-depth micro-CT analyses are pending
Xandarella spectaculum[13]	- eye bulges preserved dorsally, but are described to have been ventrally, stalked, similar to *Cindarella* and *Sinoburius*[13,85,87,88,91,93,96]	- in-depth micro-CT analyses are pending

Fig. 1 | Types of Cambrian compound eyes.
a–i, l *Pygmaclypeatus daziensis*. **a** YKLP 11427.
b Left eye of (**a**). **c, b** with interpretative drawing, arrows indicating globular facets. **d** Explanatory scheme of (**b**). **e** YKLP 13929. **f** Right eye of YKLP 13929. **g, f** With interpretative drawing. **h** Left eye of YKLP 13929. **i, h** With interpretative drawing, dotted lines indicate the material of the burst eye. **j** *Aulacopleura koninckii*[39]. **k** Compound eye of *A. koninckii*. **l** YKLP 13929, field of view indicated by whitish area. M) *Leanchoilia illecebrosa*[83] NIGPAS 115367. **n, m** with interpretative drawing. Insert: Globular facets of the stalked eye. **o** *Alalcomenaeus sp.* YKLP 11075 with 4 stalked compound eyes. Note the globular lenses/facets (arrow), (photo without arrow[38]). **p** *L. illecebrosa* with 4 stalked compound eyes. **q** Typical Cambrian trilobite, left eye (unspec. Specimen of the family Paradoxiidae). **r, q** sideview. **s** *Isoxys auritus*[28,84]. **t** Right compound eye of (**s**). **u** Schematic drawing of (**t**). **v** Globular facets of (**t**). p palpebral lobe (eye coverage), vs visual surface. Copyrights were obtained for **a–c**, **e–p**, **s–v**.
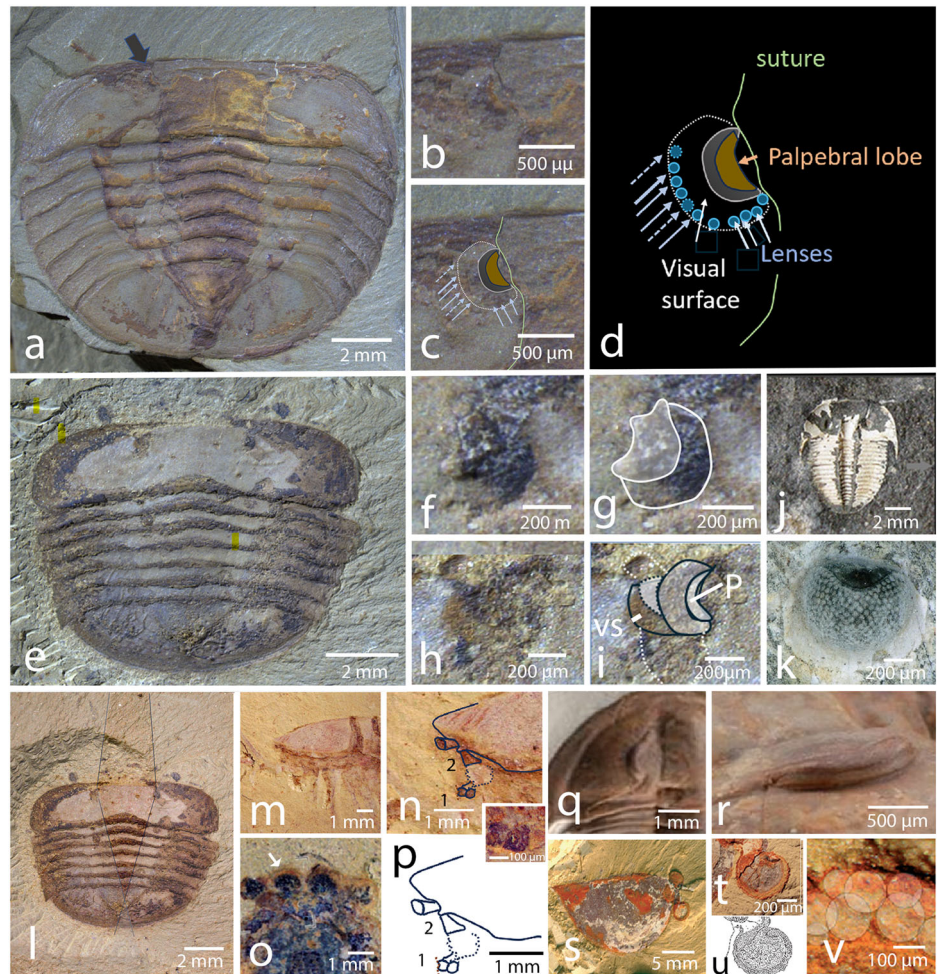

Fig. 2 | The stalked eyes of *Pygmaclypeatus daziensis*[8]. a YKLP 13929 (specimen also published in ref. [82], Fig. 20.28b) Yellow circles: protruding stalked compound eyes, white circles: dorsal compound eyes. **b** YKLP 13929 without interpretative drawings. **c1** The compound eye of **c2** *Artemia salina*[99], a primordial crustacean (Branchiopoda), about 100 mya[37], and possibly with a similar appearance as the Cambrian compound eyes with globular facets. Here the crystalline cone forms the spherical lens. **d** YKLP 13,928 (photo of the specimen from[82], Fig. 20.28a). **e** Anterior region of the cephalon of (**d**). Arrows indicate supposed stalked eyes shining through the translucent shell. **f** Dorsal compound eye of (**d**). **g, f** with interpretative drawing. **h** YKLP 13,930 (photo of the specimen from ref. [82], Fig. 20.28c). **i** Anterior region of (**h**), the white arrow indicates a dorsal compound eye, slightly distorted; the yellow arrow indicates a ventral staked compound eye, shining through the shell. **j** Compound eye of **h**), slightly distorted. **k** Interpretative drawing of (**j**). **l** Ventral articulated stalked compound eye. **m, l** with interpretative drawing. Copyrights were obtained for **a–m**.
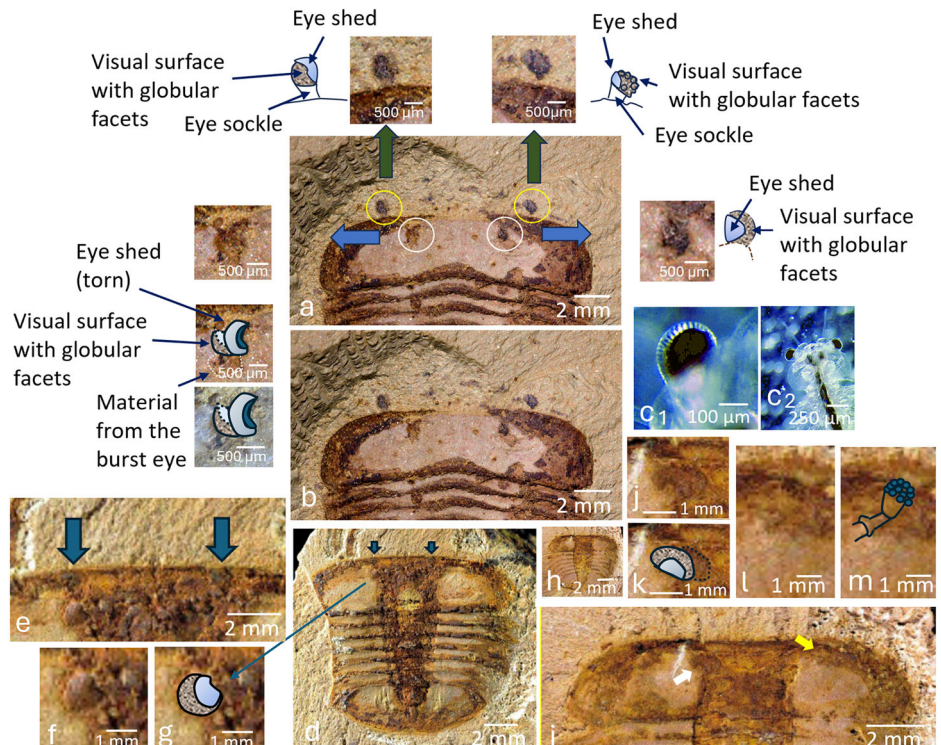
Fig. 3 | Explanatory graphics. a Structure of an apposition compound eye, consisting of numerous identical units (ommatidia). **b** Ommatidium of a terrestrial, **c** of an aquatic diurnal arthropod. **d** cross-section of an ommatidium. Note that the blue-white pattern, if focused, results in a light blue signal. **e, f** Optical axes stay vertical to the lens centres. Note that the scanning acuity of parallel optical axes is much higher than the scanning acuity in a bent visual surface. Lower part of **e** Facets of the stalked eye and their interommatidial angle. Lower part of **f** While the eyes of early Cambrian arthropods are spherical, trilobites develop more straight visual surfaces for higher acuity. **g** Eye parameter *p* as depending on luminance. Red dot: *p* of the dorsal compound eyes of *Pygmaclypeatus daziensis* (Graphic changed after ref. 10).
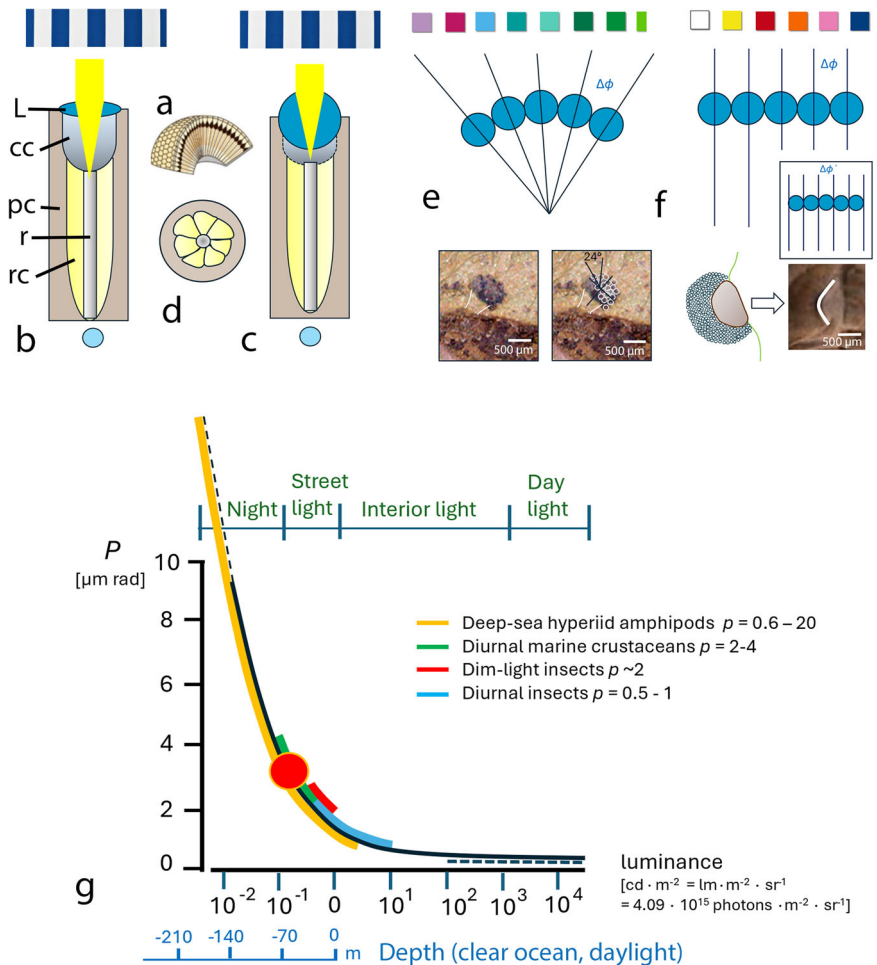
arranged in a square or hexagonal array. To resolve the two object points, the facets are to be arranged such that $\Delta\varphi = \Delta\theta/2$ (square array) or $\Delta\varphi = \Delta\theta/31/2$ (hexagonal array) when $\Delta\varphi$ is the angle between the optical axes of adjacent ommatidia[10,21] (Fig. 3e, f). In addition, Snyder described the threshold resolution of a sinusoidal grating spaced equally for the ommatidia of a compound eye working at diffraction limit when the angle of acceptance of the receptor is at optimum, with the following equation:

$$1 = 0.455\, \boldsymbol{p}\, (m^2\hat{I})^{1/2}\, \mathrm{e}^{-0.89\{(\lambda/\boldsymbol{p})^2+(\nu\Delta t/\Delta\varphi)^2\}} 13.\mathrm{eq}.18 \qquad (1)$$

With: $m^2\,\hat{I}$: 'contrast intensity parameter', describing the signal-to-noise ratio at a given light intensity, *e*: base of the natural logarithm, λ: wavelength of light, ν: relative speed of the eye related to the viewed object, Δt: integration time.

p refers to the so-called 'Eye Parameter'. *p* is defined for a square array of facets: $p = D \cdot \Delta\varphi$ [µm rad] and a hexagonal array: $p = D \cdot 3^{1/2}\, \Delta\varphi/\, 2$, with: *D* facet diameter. For blue-greenish light ($\lambda = 500$ nm), $\nu = 0$ rad s^{-1} at threshold resolution. *p* shows a curvilinear relationship[28] with the contrast intensity parameter $m^2\hat{I}$ (m modulation transfer function lens-pupil/receptor, $\hat{I}$ intensity parameter (for definition see[10,20,21] and thus with the ambient light intensity (Fig. 3). The curve provides optimal *p*-values at threshold perception of the sinusoidal grating under varying levels of illumination. These considerations are valid for systems with a single receptor per ommatidium, as typical for apposition eyes as to be assumed for *Pygmaclypeatus daziensis*. Indeed it was possible to show by refs. 29,30 that the eye parameter matches the light ecological conditions in which the investigated arthropods lived. So, the eyes of diurnal insects show an eye parameter $1 < p < 2$ [µm rad], nocturnal dragonflies show eye parameters $2\, p \le 4$ [µm rad], and eyes of deep-sea crustaceans $4 < p < 6$ [µm rad]. Many

examples confirming these results have been shown since, also for fossilized visual systems, for e.g., refs. 24,31–33. In a pioneering work for fossils, this method became particularly important because it was able to provide the first quantitative evidence that the visual system of the phacopid trilobites with their enormously large and separate lenses is different from other systems[23], which could actually be shown later[34].

Based on the newly detected eye remnants, we calculated several visual parameters to explore the conditions under which *Pygmaclypeatus daziensis* once was putatively able to see.

Results

In specimen, YKLP 11427, the dorsal eyes are preserved at ~0.93 mm length/0.7 mm width, with the palpebral lobe measuring ~0.59 mm length / ~ 0.24 mm not well enough preserved for measurements. The better-preserved left eye shows a few lenses (facets), which are visible as small, dark dots and have a diameter of around 42 µm. In total, one may estimate up to around 190 single facets per visual field (Fig. 1b, c, f–h).

In specimen YKLP 13929, both dorsal eyes are preserved. The right eye measures around 0.89 mm in length/0.74 mm in width, with the eye coverage (=palpebral lobe) measuring 0.61 mm in length/0.37 mm in width. The left eye is tilted to the side due to taphonomic processes and measures approximately 0.92 mm in length/0.62 mm in width, with the palpebral lobe measuring 0.63 mm in length/0.38 mm in width (Fig. 1e–i).

Visual properties of Pygmaclypeatus' eyes

Dorsal compound eyes. Assuming a hexagonal pattern of the facets as the densest possible arrangement, the 'Eye Parameter' *p* in *Pygmaclypeatus daziensis* results with $p = D \cdot 3^{1/2}\, \Delta\varphi/2$ to: = ~3 µm rad.

Mike Land[11] succeeded in devising a direct method to calculate the photons absorbable by a given system, thereby developing a measure of the 'Absolute Sensitivity'[11], p 480–486 of ref. [12].

The 'Absolute Sensitivity' depends on the light flux F_{abs} as absorbed by the receptor and the emitted lumens L per m^2 into each unit solid angle (steradian, sr) that is viewed by the ommatidium. [1 lumen m^{-2} sr^{-1} = 4.08 × 10^{15} photons −1 m^{-2} sr^{-1}]. F_{abs} depend on the exponential absorption of the photons along the length of the receptor x and the absorption coefficient k (fraction of light absorbed in a definite short length). It depends also on the focal length f, the aperture (lens diameter) D, and the diameter of the receptor (rhabdom) d. So in total, the absolute sensitivity $\hat{S}$ can be expressed as:

$$\hat{S} = F_{abs}/L = (\pi/4)^2 \cdot (D/f)^2 \cdot d^2 \cdot \left(1 - e^{-kx}\right)^{14eq.15}$$
$$\left[(\pi/4) \cdot D^2,\ \text{pupil diameter}\right]. \tag{2}$$

For many systems, as often for those of fossils, the length of the receptor and the focal lengths are not given, so the authors[12] give a simplified version of this equation:

$$\hat{S} = 0.62 D^2 \Delta_{\rho^{2}}{}^{15,eq.7.2} \tag{3}$$

With $\Delta\rho$ rhabdom receptor angle. $\Delta\rho$, however, in fossils very often is not known either. Snyder in ref. [10], however, for a given 'Eye-Paramter' p gives an optimal relation between $\Delta\rho$ and $\Delta\varphi$ [ref. [10], [Fig. 8]]. For $p \approx 3$ µm rad we have $p = \Delta\rho/\Delta\varphi = 0.767$, and because $p \cdot \Delta\varphi = \Delta\rho$, for $p = {\sim}3$ µm rad, and $\Delta\varphi \approx 5°$ (0.09 rad) the optimal $\Delta\rho$ is 0.069 rad (~4°). Accepting the assumption that the eye was morphologically optimal adapted, $\hat{S}$ results ~0.62 · 42^2. 0.069^2 = 5.2 µm^{2}rad.

Diurnal and surface-living arthropods often show $\hat{S}$—values below 1; for crepuscular and midwater animals, $\hat{S}$ tends to lie between 1 and 100, and nocturnal and deep-see values are found between 100 and 10,000[12]. So, the value found for the 'Absolute Sensitivity' of *P. daziensis* is in good accordance with the eye parameter, both indicating an eye adapted to low daylight conditions or a shallow-water living lifestyle close to the surface under slightly turbid, light scattering and absorbing water conditions. For comparison, extant arthropod examples can be found for a deep-sea isopod *Cirolana* sp. *(*4200 µm^2 rad^{31}), a crepuscular to nocturnal horseshoe crab *Limulus* sp. (83–317 µm^2 rad^2), a diurnal shore crab *Leptograpsus sp.* (0.5 µm^2 rad^2), or a diurnal worker bee *Apis* sp. (0.32 µm^2 rad^2)[12]. Illustrative examples of non-arthropods are the diurnal *Bufo* (toad) or coastal sea-floors inhabiting *Pecten* (scallop), both with 4 µm^2 rad[12].

As mentioned above, compound eyes work at threshold light detection and thus establish an optimized compromise between acuity (number of facets ('pixels')) as the fineness of scanning ($\Delta\varphi$, $\Delta\rho$), and sensitivity, represented by the diameter of the light perceiving structures D and the angle of light acceptance ($\Delta\varphi$, $\Delta\rho$) (Fig. 3e, f). The interommatidial angle standing for the fineness of scanning the environment optically, and the eye parameter reflecting the light ecological conditions—tell us a lot about the lifestyle of *Pygmaclypeatus daziensis*.

Finally, simply by the geometry of the compound eye, the acuity of the system can be described. The spatial frequency with which a compound eye resolves an image (represented by a sinusoidal grating again) is the 'Sampling Frequence' (YKLP 11427). It is inversely proportional to the interommatidial angle:

$$\text{'Sampling frequency'}(\nu_s) = 1/(2\Delta\varphi)^{15,eq.3.2} \tag{4}$$

With an interommatidial angle of ~5°, the sampling frequency results in ~5.6 rad^{-1}.

Ventral compound eyes. Very different from these are the small, inconspicuous, articulated stalked compound eyes (Fig. 1e, 2). These consist of an unstructured, smooth stalk consisting of several joints (Fig. 2l, m), topped by a conical unit covered by a hemispherical unit with

Table 2 | Calculated visual parameters

| Calculated visual parameters of the dorsal compound eyes (YKLP 11427)	
Visual parameter	Value
Aperture (lens diameter)	~42 µm
Field of view	~190°
Number of facets	~190 covering the whole visual surface
Interommatidial angle $\Delta\varphi$	~5° (0.09 rad)
Optimal angle of acceptance of the receptor (rhabdom) $\Delta\rho$	~4° (0.069 rad)
'Eye-Paramter' p	~3 µm rad
Absolute Sensitivity $\hat{S}$	~5.2 µm^{2}rad ^{2}
Sampling frequency ν_s	~5.6 rad^{-1}
Calculated visual parameters of the ventral stalked eyes (YKLP 13929)	
Aperture (lens diameter)	~178 µm
Field of view	variable, because of flexible and movable eye stalks, circumspectant view
Number of facets	~20
Interommatidial angle $\Delta\varphi$	~24°
'Eye-Paramter' p	~79 µm rad
Absolute sensitivity $\hat{S}$	~312 µm^{2}rad^2
Sampling frequency ν_s	~2.2 rad^{-1}

dark, globular structures. While in specimen YKLP 13929 the stalks protrude anteriorly from the dorsal shield (Figs. 11e & 2a, b). In specimen YKLP 13928 the terminal dark visual surfaces of the ventral stalked eyes can be seen shining through the headshield (Fig. 2d, e). We interpret the globes on top of the conical unit as the ommatidia of the second compound eye system, because of the globular facets being very similar to other Cambrian compound eyes, such as of *Leancholia*[35] (Fig. 1m, n, p), *Alalcomenaeus*[36] (Fig. 1o), *Isoxys*[28] (Fig. 1t–v) and others, as the dark color very probably results as relicts of the compound eye´s screening pigments such as melanin, very stable through millions of years[37]. These eyes remind of the appearance of the articulated stalked compound eyes of today's living but evolutionarily old crustaceans, about 100 million years old[37], Artemia salina103, where the crystalline cone forms nearly spherical lenses (Fig. 2c, d). Using equations as mentioned before, for these eyes ($D \approx 178$ µm, $\Delta\varphi \approx 25.7°$) the eye parameter p, ($D \cdot \Delta\varphi$) approximately reaches a value of 79.2 µm rad, the sensitivity $\hat{S} \approx 312$ µm^2 rad^2, and a sampling frequency of $\nu \approx 2.2$ rad^{-1}. These values, different from the dorsal compound eyes, indicate an adaptation to dimmer light conditions, probably, because they were worn mainly in the shadow of the headshield, scanning the ground. The different lengths of the stalks indicate the ability of a telescope-like stretching and searching in most different directions because of the missing joints, like in a snail's eyes. Some values for comparison: these eye parameter values exceed most known eye parameter values, and are only surpassed by those of *Phacops rana*, as mentioned in reference[23]. Sensitivity $\hat{S}$: *Limulus* (horseshoe crab, mainly nocturnal) 83–317 µm^2 rad^2, *Oplophorus* (deap-sea shrimp) 3300 µm^2 rad^{214}. Regarding the sampling frequency, the values are more like *Cirolana*'s than those of *Limulus*: Acuity (resolution): *Limulus* (horseshoe crab, nocturnal: 4.8 rad^{-1}), *Cirolana* (deep-sea isopod: 1.9 rad^{-1})[12].

All calculated values are summarized in Table 2.

Discussion

Different from all arthropods as far as we know, *Pygmaclypeatus daziensis* (Fig. 4) possesses two different compound eye systems—a pair of tiny dorsal compound eyes, informing about the surroundings above and on the side, and a pair of minuscule stalked eyes situated below the headshield. There have been reported arthropods with four compound eyes before (e.g.,

Fig. 4 | Three-dimensional reconstruction of *Pygmaclypeatus daziensis* showing the discovered dorsal and ventral compound eyes. a Anterior oblique view. b Dorsal view. c Dorso-lateral oblique view. d Ventral view. DCE: dorsal compound eyes. VCE ventral compound eyes.
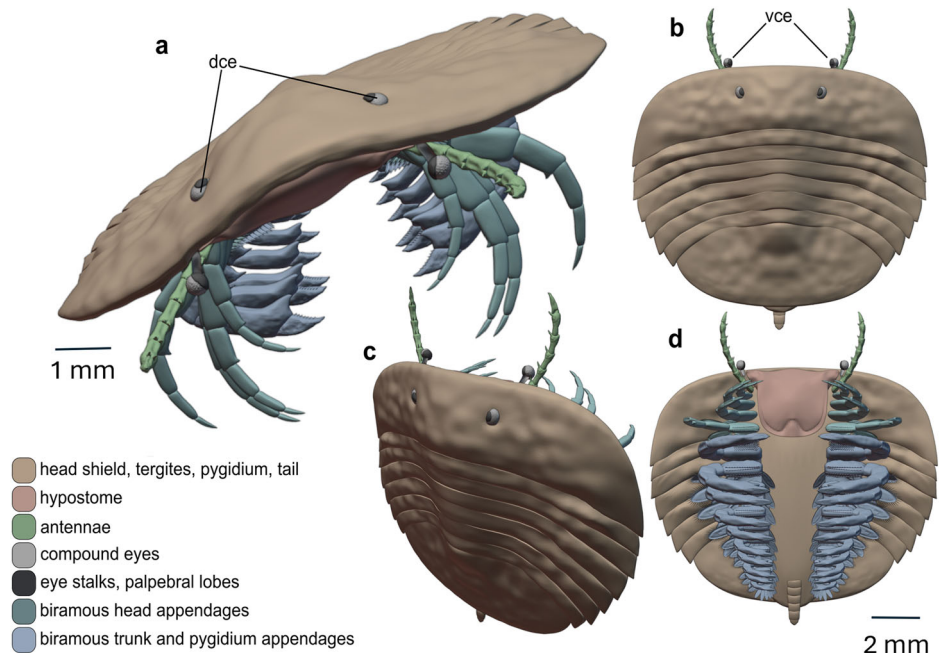
Alalcomenaeus sp[38].), but those all had two pairs of staked compound eyes, also positioned below the headshield (Fig. 1o).

Morphological characterization and visual properties of the dorsal eyes and their comparison to Paleozoic and recent compound eye systems

The dorsal eyes of *Pygmaclypeatus daziensis*, in fact, are so inconspicuous that they were not spotted at first. Despite their tiny size of just under a millimeter, they appear surprisingly elaborate. Contemporary trilobite eyes, which are slit-shaped and with exceptions, such as *Holmia*[3], Early Cambrian trilobite eyes at their surface generally showed no facets (Fig. 1q, r). The dorsal eyes of *P. daziensis* have the shape of a hemispherical segment, stabilized dorsally by a crescent-shaped lid (the so-called palpebral lobe). We find exactly the same shape of compound eyes in later occurring trilobites as, for example, the Silurian, very conservative *Aulacopleura koninckii*[39] (Fig. 1j, k). In specimen, YKLP 11427, traces of equally sized facets have been preserved so that one can estimate that the entire surface of the eye may have contained about 190 facets ('pixels'), each with a diameter of ~40 μ (Fig. 1a–d).

The almost hemispherical eyes open a wide visual field—upwards, what for example is untypical for coeval early Cambrian trilobites, whose eyes are scanning the horizon (Fig. 1q, r) just laterally; laterally *P. daziensis*' field of vision covers an area of 2× ~190° (Fig. 1l), scanning the environment around the arthropod. This is enormously wide, e.g. compared to the trilobite *S. reetae*[18] showing just 2× ~120°, as typical for many Cambrian trilobites[19].

We do not know anything, of course, about neuronal properties. It is well known that to higher the sensitivity in many arthropods a pooling of the signals on neuronal level is possible[40] nevertheless, we can assume that the dioptric apparatus is already optimally adapted to the external constrains.

These qualities alone tell us a lot about the lifestyle of *Pygmaclypeatus daziensis*. The results suggest that *Pygmaclypeatus daziensis* possessed dorsal compound eyes that were well adapted to moderate light conditions. The eye parameter of ~3 μm rad and an 'Absolute Sensitivity Ŝ' of ~5.2 μm² rad² indicate that *Pygmaclypeatus daziensis* was active during the day or even during the rising dawn (Fig. 3g). It probably lived as a surface water inhabitant in slightly turbid water.

The wide interommatidial angle (~5°) tells us that, at the expense of acuity, the eye was built to capture as much light as possible. With an interommatidial angle of ~5°, the sampling frequency results in ~5.6 rad^{-1}. The acuity of other arthropods for comparison: *Aeschna* (dragonfly, diurnal and hunting over calm waters) 115 rad^{-1}, worker bee 30 rad^{-1}, crab *Leptograpsus* 19 rad^{-1}, *Limulus* 4.8 rad^{-1}, *Cirolana* (deep-sea isopod) 1.9 rad^{-1}[12] and quite low in particular compared to the Jurassic diurnal ambush predator *Dollocaris ingens*[22]. For comparison, this predatory crustacean has ~18,000 facets, a facet diameter of ~40 μm, an interommatidial angle of ~1°, and a sampling frequency of ~20 rad^{-1}[27].

There is a principal difference between the concept of prey and predator's eyes, not just among arthropods. Predators need eyes that are good at spotting and recognizing objects before investing energy in hunting them. They have eyes with a high resolution and an overlapping field of view, providing three-dimensional vision and the capacity to estimate distances[41]. One may easily conceive that for prey, it is vital for survival to perceive everything that moves around them, as potential threats by predators. Their eyes provide a wide field of view, while a high resolution for a distinct analysis of the environment is of less importance. *Pygmaclypeatus daziensis* shows the second type of eye—less than ~190 'pixels' (= facets) spread over the whole visual surface inside a range of 190° form a rough, imprecise image, and just offers a rough impression about the light distribution of the environment. But these eyes are excellent movement detectors, as the illumination of one facet after the other is changed by any object passing by. This allows the organism to escape from any disturbance in an otherwise calm and homogeneous visual environment. The visual field is overlapping here twice—once in the back, but here the rachis might be insurmountable, so this property is probably useless, the other overlapping field of view is a little more than a body length in front of the animal, but because of the low resolution of the eye just a very rough estimate of the distance might be possible, if at all. No contemporary trilobite would be endowed with such a field of vision.

Thus even if this eye of *Pygmaclypeatus daziensis* is very small, it provides an excellent optical alarming system.

The interommatidial angle $\Delta\varphi$ of ~5° indicates a scanning of moderate quality of the surrounding, and not many items can be resolved because all details inside of ~5° are summed up to one 'average' signal per facet. In comparison: in a high-resolving eye of the predatory dragonfly (*Aeschna*) $\Delta\varphi = 0.25°$[12], the eye of a bee (*Apis*, worker) shows 0.95°, *Ephestia* (moth, nocturnal insect) $\Delta\varphi = 2.7$ (Land.[11])[4]. The sampling frequency represents the same. *Pygmaclypeatus daziensis* shows a ν_s = ~5.6 rad^{-1}, which is better

than that of the light-limited deep-sea crustacean *Cirolana* (1.9 rad^{-1}). The resolution is similar to that of the crepuscular to nocturnal horseshoe crab *Limulus* (4.8 rad^{-1})[11,12], but worse compared to the diurnal ambush predator *D. ingens* (Crustacea) with $v_s \sim 20$ rad^{-1}[27] or the predatory dragonfly *Aeschna* $\Delta\varphi = 115$ rad^{-1}[11,12].

The neural superposition compound eye of *Drosophila melanogaster* L. may also provide an interesting comparison. The flying insect is highly visual and has an interommatidial angle of ~3.8°–5°[12,42–44]. The sampling frequency of *Pygmaclypeatus* eyes is of the same range, but the ecologies of fruit flies and the benthic *P. daziensis* are highly different. Because the fruit fly is not a predator for which it is necessary to identify its prey clearly, the eyes are primarily necessary for flight stabilization and orientation. One may assume that the latter applies to the eyes of *P. daziensis* also, even if the environment and lifestyle of both arthropods are different. To find and recognize nutrients chemoreception may be involved as an important factor in both species.

We see that the dorsal compound eyes of *Pygmaclypeatus daziensis* are adapted to moderate light conditions (daylight—dawn, $p = \sim 3.6$ μm rad), and are hardly image-forming systems (relatively wide interommatidial angle ~5°, sampling frequency $v_s \sim 5.6$ rad^{-1}). Their wide field of view (~190°) supports the assumption that these minuscule eyes (~1 mm) had the potential to work as excellent movement detectors over a wide field of view.

Although these eyes were tiny, they may have provided an effective predator detection, potentially with a significant selective advantage. According to Chen[45], p.15, the Chengjiang biota inhabited water depths of 70–120 m, corresponding to the lower sublittoral or circalittoral zone, characterized by moderate to weak light conditions. In these depths, minimal sunlight penetrates, rendering photosynthesis ineffective except for some red algae. Additionally, recent research by Saleh and colleagues[46] suggests that the Chengjiang biota thrived in a deltaic environment marked by fluctuating salinity levels and frequent storm floods, resulting in high sedimentation rates. Despite these conditions, the water likely remained oxygen and nutrient-rich.

Ultimately, based on our analyses, the following autecological picture can be suggested for *Pygmaclypeatus daziensis*: This small arthropod possessed minuscule eyes adapted to moderate light conditions. The eyes were designed to capture as much light as possible, sacrificing acuity for light sensitivity, and equipped with the capacity to serve as excellent motion detectors, potentially providing an efficient optical alert system. The eye parameter and sensitivity results may indicate an adaptation to the turbidity of the water under daylight conditions.

With its motion-detecting eyes this arthropod probably was capable of escaping from any disturbance in an otherwise calm and uniform visual environment. *Pygmaclypeatus daziensis* was primarily active during the day in turbid water or during the dawn. Because the results of the eye parameter and the 'Absolute sensitivity' stay at the transition between values indicating adaptations to daylight and dimmer light conditions, *P. daziensis* may have been adapted, for example, to turbidity of the water under daylight conditions. Also, it may have inhabited deeper waters or thrived in turbid or mixed environments. Although the facets of specimens YKLP 13928, YKLP 13929, and YKLP 13930 are less distinct than in YKLP 11427, they show similar dimensions. Since the dorsal eyes are very similar in all four specimens, it seems evident that although the data could only be obtained from two different individuals, the two systems (dorsal and ventral eyes) are different in terms of their adaptation patterns.

Morphological characterization and visual properties of the ventral eyes and their comparison to Paleozoic and recent compound eye systems

Very different from the dorsal eyes are the jointed (Fig. 2l, m), probably very flexible and movable ventral stalked eyes, which, as long as they were held under the headshield, were presumably supported by chemosensorics. The ventral stalked eyes may have investigated the ground for prey such as worms, other small organisms, and organic nutrients actively. Protruding

from the margins of the headshield, they may have 'looked around'. Covered by the eyelid, a view inside was blocked, and so just as one may assume, the closer anterior-lateral surrounding was explored. This may have been a good complement to the information from the dorsal eyes, which probably provided a visual field with a distance perspective.

Because the circle of the headshield shadows them, these are more sensitive and adapted to lower light conditions. Their lower resolution surely is a sacrifice to this sensitivity but may have been sufficient enough to trace up small living prey such as worms or arthropod larvae, dead organic material, or algae.

Thus, considering the physiology of the eyes and the morphology of the appendages together, this suggests the first evidence ever for an arthropod with two different pairs of compound eyes in any early Cambrian Chengjiang taxon of the non-trilobite Artiopoda group, if not of any arthropod. Even though the eyes are small and inconspicuous, we find a highly specialized, efficient visual system that is uniquely and optimally adapted to the life needs of this early Cambrian artiopod, more than half a billion years old.

Regarding all statements that were possible in this study by the eye-morphology of *P. daziensis* alone, there remains one major problem with such inferences–it is the possibility of neural processing such as summations that could completely transform the properties such as sensitivity and resolution (overview see ref. 47) in which we are interested. We may assume, however, that many of these mechanisms represent modern adaptations to special ecological conditions that were not yet developed in the Cambrian at the time of the appearance and beginning of differentiated eye systems. They probably will not have occurred before the Cambrian-Ordovician boundary or the Ordovician itself, when the great radiation and invasion of new ecological niches began and new eye systems evolved, for e.g., ref. 48.

Extant compound eyes and comparison with Pygmaclypeatus
The presence in *Pygmaclypeatus* of one specialized eye each for looking up and one for looking down is thus a unique feature previously unknown in artiopods.

To possess two different eye-system is typical for all euarthropods. They have one pair of lateral eyes (in Myriapodes and Chelicerata homologous to compound eyes[49] and a second ocular system, the so-called median eyes (2–4 median eyes)[32]. The median eyes, however, are not compound but so-called 'simple eyes' (ocelli) with a single lens focusing the light onto a retina flooring a small cellular cup. *P. daziensis* misses such ocelli—both ocular systems are compound eyes.

The median eyes are considered homologous to the eyes of the ecdysocoan onchophora and fossil lobopodians[50,51], and possibly older than the compound eyes. Thus, it is rather probable that arthropods originally possessed just two median eyes, as did the eurypterids, and still do the chelicerates. Possibly by gene duplication *sensu* Gehring[52,53], some Cambrian arthropods developed 4 median eyes (*Cindarella eucalla*[54], the leanchoiliids and still today the phylogenetically old group of the crustacean phyllopods[35,55–57]. In some leanchoiliids can be observed that the median eyes fuse, so result just three median eyes, to become typical for trilobites[58] and pancrustaceans (hexapods and crustaceans), except the Phyllopoda as mentioned. These observations bring us closer to understanding the enigmatic relationships of the 5 stalked eyes of the Middle Cambrian *Opabinia regalis*[59], from the Burgess Shale, Canada. Here we rather probably observe 3 median eyes and 2 stalked lateral eyes. That the median eyes are stalked, too, is probably unique, and whether the lateral eyes are compound is probable, but still an interesting and enormously important point to investigate.

Other principles in recent eyes to achieve differentiation of visual performance
The basic principle–adaptation to two specific visual environments in one animal, however, is commonly found in extant arthropod compound eyes. They may occur during eye development to facilitate a shift of habitats[60,61], and also as regionalization within the compound eye. For example, in dragonflies (Odonata), dorsal, ventral, and larval eye regions exist, each characterized by specific shapes of the ommatidia's dioptric apparatus and
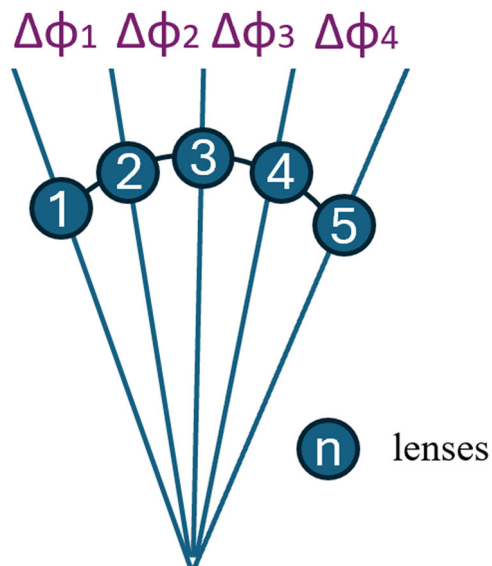
Fig. 5 | Determination of the interommatidial angle $\Delta\varphi$. For an explanation, see the text above. lenses.

rhabdoms[62]. Moreover, the dorsal rim area of many insect compound eyes is composed of ommatidia adapted to polarization vision and orientation along the celestial *e*-vector pattern[63], and in decapod crustaceans, ommatidia of different chirality are found dorsal and ventral to the eye equator[64].

Of peculiar interest as compared to *Pygmaclypeatus* are insects with 'double' compound eyes, viz., some groups of mayflies (Ephemeroptera), and whirligig beetles (Gyrinidae) as they also exhibit an eye-specific functional differentiation. In males of *Baetis* and some other mayflies, a pair of dorsal turban eyes exists, functioning as a clear zone superposition eye, while the lateral compound eye is an apposition eye[25,65]. Correspondingly, whirligig beetles have dorsal compound eyes adapted to vision in air and ventral eyes adapted to vision in water[66,67], each with specific features even to the level of corneal nanocoating[68]. In both mayflies and whirligig beetles, the double compound eyes are referred to as split eyes, i.e., the outcome of one-eye primordium rather than two. At the level of the optic lobes of the lateral protocerebrum, both have split lamina and medulla (first and second-order) neuropils innervated to a single lobula (third order visual neuropil)[65–67]. As early as 1916, Priesner[69] described the differentiation of the turban eye from a cluster of embryonal cells at the edge of the larval lateral eye undergoing novel mitotic waves in later larval stages thus supporting the idea of a one-eye-origin.

No fossilized residuals of optic lobes are available at the moment in *Pygmaclypeatus*. Therefore, we cannot say whether or not the double compound eyes of this artiopod are of the 'split' type. The physical distance between both eyes, the stalked and the sessile dorsal ones, is much bigger than of those in mayflies and whirligig beetles, i.e., they have strongly differing positions on the headshield. However, this is not a sufficient condition to infer completely separated 'double' neural optic lobes in this artiopod. Instead, the universal association of arthropod compound eyes with the lateral protocerebrum suggests that also in *Pygmaclypeatus*, a 'focus' visual neuropil might exist, with which both eyes are connected. Following the ideas of Tanaka and coworkers[38] for *Alalcomenaeus*, this would be the second visual neuropile.

Additionally, considering the new insights into the morphology, especially that of the appendages, as revealed by Schmidt and colleagues[13], a picture emerges suggesting that *Pygmaclypeatus daziensis* could potentially have been pushing off with the walking legs and floating over the sea floor, searching for most diverse organic material, such as worms, decayed organisms or algae material. It may even have been able to 'glide' and hover over the sea floor with the paddle-shaped lamellae of its trunk exopodites[9], similar to *Naraoia compacta*[59] (compare[70]). The flat body, in particular,

makes it insensitive to currents and changes in flow. It also may have had the potential to burry in the sediment, for hiding or resting, with only its eyes protruding from the sand. This would explain the heteronomous appendages throughout the body: the four head appendages shared a walking leg-like endopodite with a sharp terminal claw, as well as a reduced, stenopodous exopodite with unknown function. On the other hand, the trunk appendages had more robust endopodites, terminating in a somewhat subchelate terminal podomere[31], p.8, to suggest that these appendages might have been used for burrowing, aside serving an anchoring/grabbing function. Furthermore, the exopodites of the trunk appendages were flap-like or lamellate, presumably aiding in ventilation. Given this specific and precise ventral morphology–*Pygmaclypeatus daziensis* may have used its trunk appendages to burrow itself into the sediment to hide from predators, and the inconspicuous dorsal eyes above the surface to observe when the threat may have abandoned. While similar subchelate structures showed to be useful in grabbing and anchoring[71–73], flattened and broadened terminal podomeres of an appendage in general do help in burrowing as well[74,75].

Conclusions

Probably unique in the arthropod realm, the non-trilobite artiopodan arthropod *Pygmaclypeatus daziensis* from the Lower Cambrian Chengjiang fauna of South China possessed two pairs of compound eyes—one sessile pair, dorsally on the headshield, in a position comparable to the closely related trilobites. It may also be mentioned that such sessile eyes if they possess lateral eyes (compound eyes), are also present in modern myriapods and chelicerates. Examples of the latter are *Limulus* (Xyphosura) and the fossil eurypterids[76]. One pair of stalked eyes ventrally, can be seen in for instance early Cambrian *Leanchoilia* sp[35]., *Tanglangia* sp[77]., or *Jianfengia* sp[78]. However, those represent taxa with elongate, rather lateral body organizations, and don´t cluster among Artiopoda [sensu13].

The estimation of specific visual parameters based on recently discovered minuscule eyes of four fossilized *P. daziensis* specimens from the Chengjiang biota, China, provides insights into the former lifestyle of these organisms, thus offering additional information to complement the existing in-depth micro-CT analyses of the ventral morphology. While tiny, articulated stalked, ventrally located eyes are typical for many non-trilobite antipodean arthropods, suggesting a bentho-pelagic, predatory lifestyle (e.g., *Cindarella eucalla*[79] or the typical, purely pelagic *Isoxys*[2,80], unstalked, minuscule eyes located dorsally on the headshield are rather atypical and have not been previously assumed. These dorsally located compound eyes are typical, however, for trilobites, which may give *Pygmaclypeatus daziensis* regarding the eyes a phylogenetically intermediate position between trilobites and non-trilobite artiopods—a non-missing link. Future research on yet previously suspected 'eyeless' species (e.g., *Acanthomeridion serratum*[81], *Squamacula clypeata*[13] may bring light to this matter, shedding light in the dark on our understanding of the visual systems of early Cambrian euarthropods from the renowned Chengjiang biota of South China.

Material and methods

We reinvestigated four specimens of Pygmaclypeatus *daziens*: YKLP 11427, YKLP 13928, YKLP 13929, YKLP 13930. Specimen YKLP 11,427 was originally micro-CT analyzed and published in ref. 9, Fig. 1. Specimen YKLP 13928 was originally published and figured in Hou et al. (fig. 20.28a)[82]; in ref. 11, fig. 2 only micro-CT results were shown. Specimen YKLP 13929 was originally published and figured in ref. 82 Fig. 20.28b; in Schmidt et al.[9] (extended data Fig. 1)[4] it was analyzed via micro-CT and refigured. Specimen YKLP 13930 yet was only published and figured in ref. 82, Fig. 20.28c. Photographs of specimens YKLP 13928 and YKLP 13930 reprinted with permission. Photography under ambient light conditions for specimens YKLP 11427 and YKLP 13939 was conducted using either a Canon EOS 5DSR camera (DS126611) equipped with an MP-E 65 mm macro photo lens or a Keyence VHX-5000 digital microscope. All specimens are preserved in dorsal view and replicated in pyrite and/or iron oxides

Fig. 6 | Illustration of the method to estimate the approximate interommatidial angle $\Delta\varphi$ for the dorsal eye of the specimen YKLP 1127. For an explanation, see the text above. Copyrights were obtained for the photographs in Fig. 6.
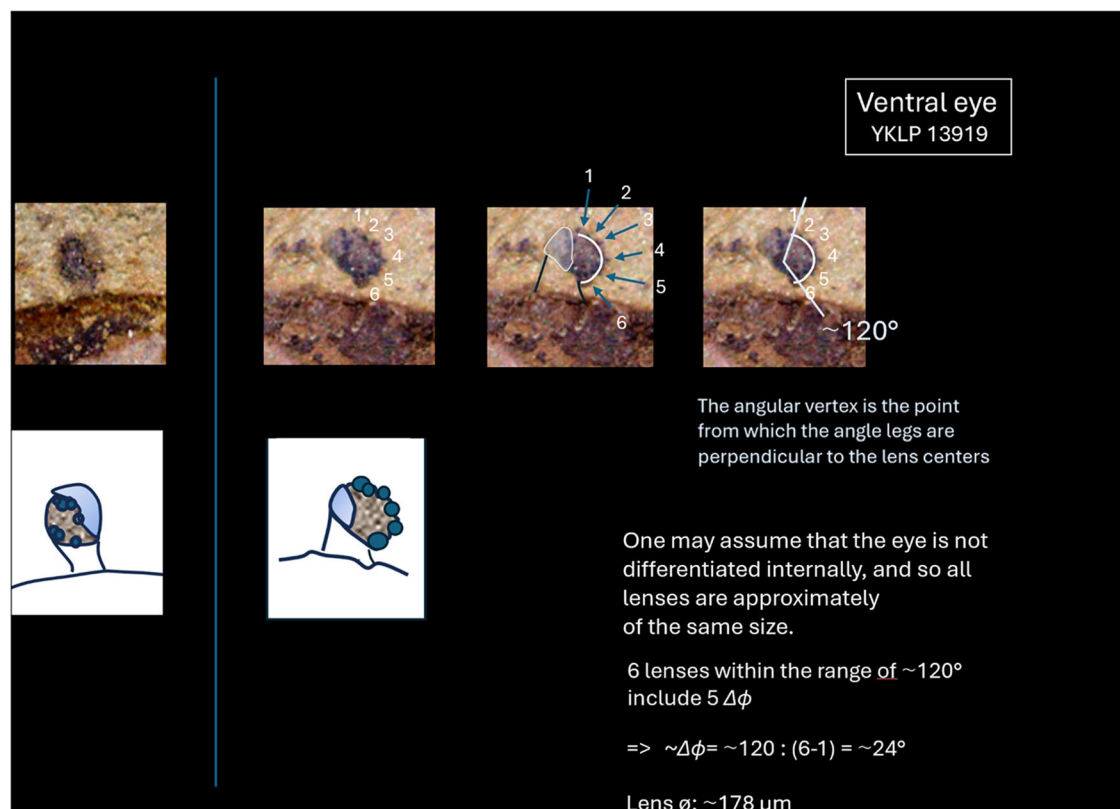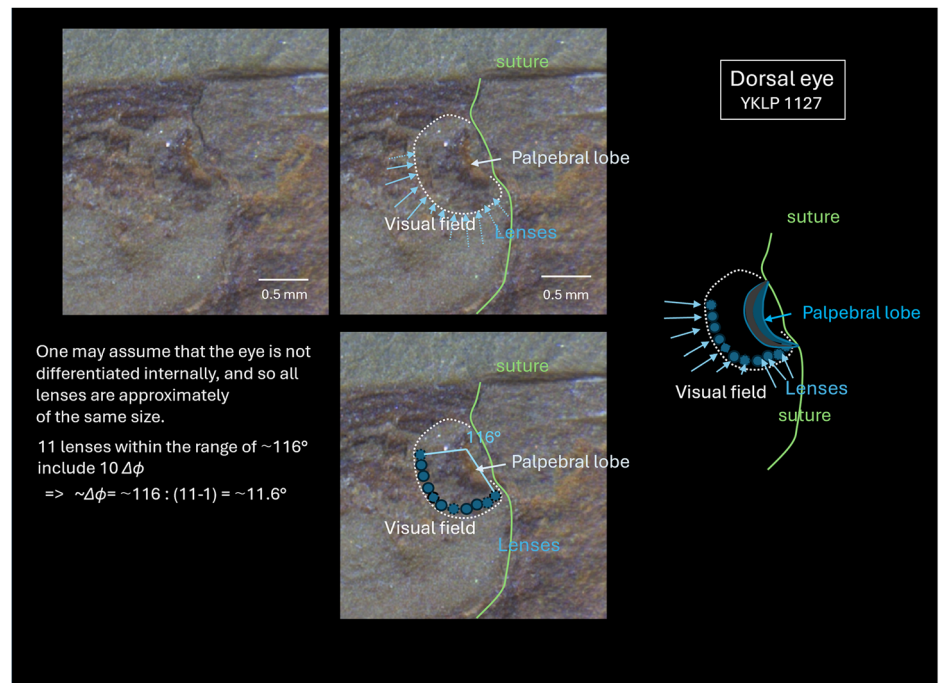

Fig. 7 | Illustration of the method to estimate the approximate interommatidial angle $\Delta\varphi$ for the ventral eye of the specimen YKLP 1127. For an explanation, see the text above. Copyrights were obtained for the photographs in Fig. 7.

(a preservation method commonly observed in fossil euarthropods from the Chengjiang Lagerstätte). Eyes could be detected on all specimens.

The following visual parameters were calculated: field of view, absolute sensitivity $\hat{S}$, 'eye-paramter' p ($p = D \cdot 3^{1/2}\, \Delta\varphi / 2$), interommatidial angle $\Delta\varphi$, sampling frequency ν_s. Three-dimensional reconstruction created with Blender vers. 4.

Provenance of the here described and investigated specimens: *Pygmaclypeatus daziens*: YKLP 11427, YKLP 13928, YKLP 13929, YKLP 13930.

All specimens, collected from the Yu'anshan Member, Chiungchussu Formation, Dazi section, Early Cambrian of Haikou, Yunnan Province, South China, are housed at the Yunnan Key Laboratory for Palaeobiology at Yunnan University, Kunming.

Other specimens: *Alalcomenaeus sp* YKLP 11075, Yu'anshan Member, Heilinpu Formation, Early Cambrian, Yunnan, China, housed at the Yunnan Key Laboratory for Palaeobiology at Yunnan University, Kunming, China; *Aulacopleura koninckii* (Barrande 1846) Špičatý Hill Loděnice, Motol Formation,, *Cyrtograptus lundgreni*-Zone, Silurian, Wenlock, Homerian, Czech Republic, GIK 191, Geological Institute University of Cologne; *Leanchoilia illecebrosa* (Hou[83]), NIGPAS 115363, Yu'anshan Member., Heilinpu Formation, Early Cambrian, Xiaolantian, Yunnan, China, housed at the Yunnan Key Laboratory for Palaeobiology at Yunnan University, Kunming, China. *Isoxys auritus* (Jiang[84]) YKLP 11043, Yu'an-shan Member., Heilinpu Formation, Early Cambrian, Mafang, Yunnan, China, housed at the Yunnan Key Laboratory for Palaeobiology at Yunnan University, Kunming, China.

Methods used to estimate the properties of the eye of *Pygmaclypeatus daziensis* Zhang, Han, and Shu,[79]

Specimens of *Pygmaclypeatus daziensis* Zhang, Han, and Shu[8] are very rare, and therefore, only a few specimens in sufficiently good condition are available to us. We are aware that the statements we make only describe this particular individual's characteristics. Still, nevertheless, it is a representative of its species and adapted to the living conditions surrounding it. We are also aware that the state of preservation of these systems, which are over half a billion years old, is not as good as that of recent material, which is often available in any number and selection. Therefore, the evaluations made here are estimates and approximations, but they certainly provide insight into the visual system's previous natural conditions.

The field of view was approximated by finding the angle between the outer lenses in the visual field, the arms of this angle standing vertically on the centers of these lenses.

The diameter of the lens of the ventral eye was determined as the mean of individual measurements of lenses from magnified high-resolving photographs. The lens diameter of the dorsal eye was estimated as an average of the number of clearly visible lenses within a certain distance of the visual surface.

The determination of the interommatidial angle $\Delta\varphi$ (Fig. 5) is also based on enlarged high-resolution photographs and was determined graphically, as shown in the figures below (Figs. 6 and 7) in specimens in which the lenses were clearly visible on the curved outer surface of the eye. A comprehensive angle was set between a certain number of lenses so that the arms of the angle are perpendicular to the center of the outermost lenses; the apex of the angle then results automatically. One can observe that all lenses have more or less the same size, and the comprehensive angle formed this way always includes one $\Delta\varphi$ less than the number of lenses indicates. So, we can get an average of the $\Delta\varphi$s over the entire range of the angle (see below).

Data availability

All data can be found in the manuscript and supplementary information. Materials used in the analysis will be available to any researcher for the purpose of reproducing or extending the analyses. The analyzed, here described and investigated specimens: *Pygmaclypeatus daziens* Zhang et al.[8]. YKLP 11427, YKLP 13928, YKLP 13929, YKLP 13930 were all collected from the Yu'anshan Member, Chiungchussu Formation, Dazi section, Early Cambrian of Haikou, Yunnan Province, South China, and are stored at the Yunnan Key Laboratory for Palaeobiology at Yunnan University, Kunming.

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Author contributions

M.S., B.S., and Y.L. designed the research. B.S. discovered the second dorsal eye system, calculated the visual parameters, and supervised the project. X.H. and Y.L. secured the funding. X.H. collected the material. M.S., B.S., and R.R.M. wrote the paper with input from all the other co-authors. All authors participated in the interpretation of the findings and the discussions and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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