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Agnostid trilobites from the Arenig–Llanvirn of South China

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ABSTRACT: Agnostid trilobites are relatively abundant and taxonomically diverse in outer shelf facies of the Yangtze Platform and Jiangnan Transitional Belt regions of the South China Plate. Nine Arenig and Llanvirn species, representing at least five genera or subgenera in the Agnostidae, Diplagnostidae and Metagnostidae, are treated in a taxonomic review of the South Chinese Agnostida, based on new material from the Dawan and Kuniutan formations of W Hubei and the Zitai and Jiuxi formations of N Hunan. The new genus *Han* is established to incorporate the globally youngest known diplagnostid species. The new species *Han solo*, *Geragnostus* (*Geragnostus*) *balanolobus* and *G.* (*G.*) *waldorfstatleri* are established. *G. carinatus* is recognised as being based on inaccurately interpreted material, and is only tentatively retained within *Geragnostus*. Three further taxa represented by poorly preserved material are left in open nomenclature. The geographic distributions of different agnostid species across the South China Plate, and the endemicity to the palaeoplate displayed by all Arenig–Llanvirn South Chinese species, suggest that these agnostids at least were either benthic or epibenthic.

KEY WORDS: *Geragnostella*, *Geragnostus*, *Han*, Hubei, Hunan, *Micragnostus*, Ordovician, *Trinodus*.

Agnostid trilobites are a characteristic component of many Chinese open marine facies during the Lower Palaeozoic. They are abundant in Cambrian strata, but undergo a global decline throughout the Ordovician, with reduced abundance and diversity and longer stratigraphic ranges as compared to Cambrian taxa (Nielsen 1997), and eventually disappear during the end-Ordovician mass extinction. This pattern of Ordovician decline is characteristic of those trilobite families assigned to the Ibex Fauna by Adrain *et al.* (1998). However, although generally a very minor component of Ordovician trilobite faunas (Nielsen 1997), agnostids remain relatively frequent in many Chinese outer shelf facies throughout the system. Zhou (1987) recognised 43 species and subspecies of Chinese Ordovician agnostids from 54 available in the pre-1985 literature; these were reassigned to nine genera representing at least four families, but primarily to the Metagnostidae. Nielsen (1997, 1999) listed 92 Chinese Ordovician agnostid taxa (material described as species or listed under open nomenclature), but made no effort to revise species or disclose species synonymy.

Extensive new Arenig–Llanvirn trilobite collections from Hubei and Hunan indicate that agnostids remained an important component of outer shelf trilobite associations in the Yangtze Platform and Jiangnan Transitional Belt regions of the South China Plate during the Arenig and Llanvirn. These collections form the basis for a revision of the agnostid taxa occurring on the South China Plate during this interval. This helps to start addressing the many problems of Ordovician agnostid systematics highlighted by Nielsen (1997, 1999), and also forms part of a series of publications by the present author on the taxonomy, palaeoecology and biogeography of South Chinese trilobites (see also Turvey 2005a, b; Turvey & Zhou 2002, 2004a, b).

1. Material and methods

Approximately 130 agnostid specimens, representing at least five genera or subgenera in the Agnostidae, Diplagnostidae and Metagnostidae, form part of a larger trilobite collection obtained by the present author in September–November 1998. Agnostids were collected from the Dawan Formation (Arenig) and Kuniutan Formation (Llanvirn) at Daping, W Hubei, the Zitai Formation (Arenig) at Shuanghong and Maocaopu, N Hunan, and the Jiuxi Formation (Arenig–Llanvirn) at Baimaquan and Panjiazui, N Hunan (Figs 1, 2). Stratigraphic correlation between these formations is summarised in Figure 3; further information on named formations and localities, and on stratigraphic terminology employed herein, is given in Turvey & Zhou (2002, 2004a) and Turvey (2005a).

2. Systematic palaeontology

The terminology used herein follows that of Whittington & Kelly *in* Kaesler (1997) (although note the alternative morphological interpretation and terminology employed for pseudagnostine pygidial characters by Peng & Robison 2000). All material figured herein is deposited in the Nanjing Institute of Geology and Palaeontology (NI); additional non-figured material is deposited in the University Museum, Oxford (OUM) and the Natural History Museum, London (NHM). Repositories of described or cited specimens also include the Xi'an Institute of Geology and Mineral Resources (XI).

Order Agnostida Salter, 1864
Family Agnostidae M'Coy, 1849
Subfamily Agnostinae M'Coy, 1849
Genus *Micragnostus* Howell, 1935

Type species. *Agnostus calvus* Lake, 1906; Tremadoc Stage, Nant Rhosddu, Arenig, N Wales, UK. By original designation.

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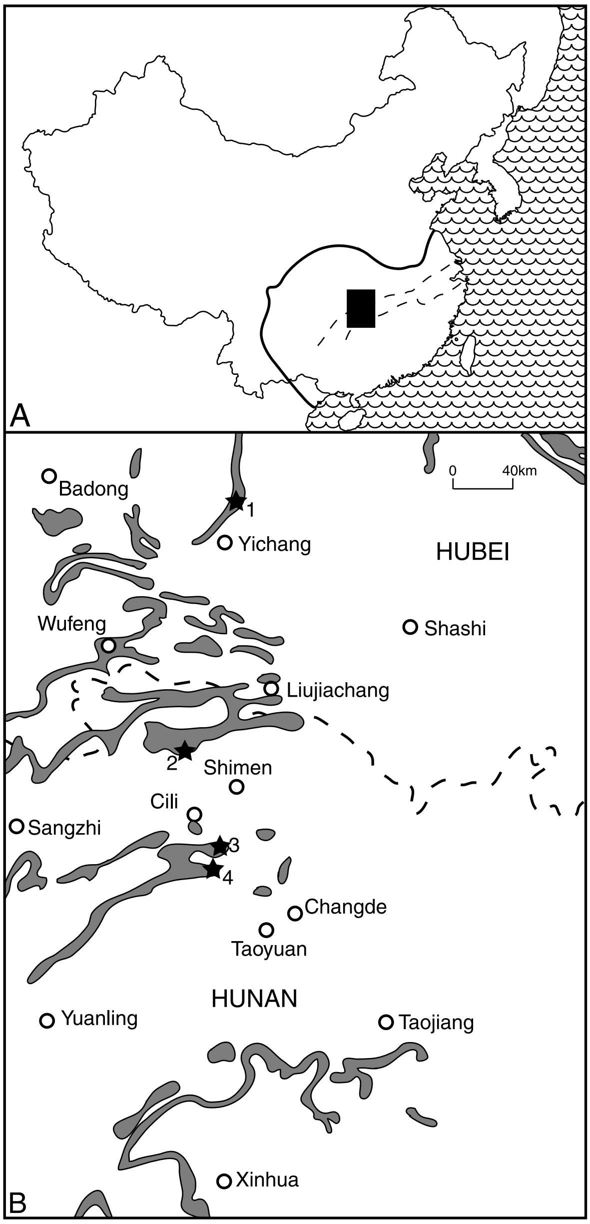

Figure 1 (A) Map of China, showing modern location of the South China Plate, with division from modern-day northwest to southeast into the progressively deeper-water facies of the Yangtze Platform, Jiangnan Transitional Belt and Zhujiang Basin, and with location of the study area indicated. (B) Enlargement of the highlighted region of W Hubei and N Hunan, showing geography of collection localities mentioned in the text. Ordovician outcrops are in grey, localities are indicated with stars, and province boundary indicated with dashed lines. Key: 1 = Daping, 2 = Shuanghong, 3 = Maocaopu, 4 = Baimaquan and Panjiazui. Geographic data from the Bureau of Geology and Mineral Resources of Hunan Province (1988) and the Bureau of Geology and Mineral Resources of Hubei Province (1990).

Micragnostus? sp.
Figure 4a–b

Material. One cephalon (NI 133786), one pygidium (NI 133787).

Occurrence. Bed 2, Zitai Formation, Shuanghong, Baiyun, Shimen County, N Hunan, China.

Remarks. An agnostid cephalon from Shuanghong displays a prominent F3 glabellar furrow. It is probably assignable to *Micragnostus* rather than *Anglagnostus* Howell, 1935, the only other Arenig agnostid with a similar F3 condition, because the glabella occupies 65 per cent of the cephalic length, whereas *Anglagnostus* is diagnosed as having a shorter glabella (Nielsen 1997). A poorly preserved agnostid pygidium from the same horizon, unassignable to the other agnostid species present at Shuanghong, appears to show the narrow border furrow typical of *Micragnostus*, unlike the deep, broad condition displayed in metagnostids (see Fortey 1980), and may represent the same species. However, Nielsen (1997) diagnosed *Micragnostus* as having a fairly narrow glabella, whereas that of the new cephalon is very broad. Although the new cephalon is rather poorly preserved, and fine morphological details such as the position of the glabellar tubercle cannot be determined, this character serves to distinguish it from other Arenig *Micragnostus* species (e.g. compare with Fortey 1980: pl. 1). Although Peng (1990) classified *Anglagnostus* as a subgenus of *Micragnostus* on the basis of the distinct transglabellar furrows displayed by both genera, Nielsen (1997, 1999) regarded this character state as plesiomorphic for the Agnostidae, and so it is not even certain whether the new agnostid is closely related to *Micragnostus*. However, as the new Zitai Formation taxon is so poorly known, it seems preferable to assign it with reservation to this genus.

There has in the past been some confusion in the literature over the taxonomic differences between *Micragnostus* and *Geragnostus* Howell, 1935, leading to uncertainty over the taxonomic diversity of the former genus during the Early Palaeozoic (see e.g. the assignment of *Geragnostus* (*Geragnostella*) *fenhsiangensis* Lu, 1975 to '*Micragnostus* (*Anglagnostus*)' by Peng 1990). The two genera are now placed within two separate families (Fortey 1980; Shergold *et al.* 1990; Nielsen 1997, 1999), and *Micragnostus* is known to display much lower species diversity during the Arenig than during the Cambrian or Tremadoc. Nielsen (1997, 1999) only confidently recorded three different *Micragnostus* species from the lower Arenig, and the genus does not appear to be present in geologically younger horizons. The new species represents the first record of *Micragnostus* from the Arenig of South China, although species tentatively assigned to the genus by Nielsen (1997, 1999) have been recorded from the Tremadoc of the region (Chien 1961; Lu & Lin 1984).

Family Diplagnostidae Whitehouse, 1936
Subfamily Pseudagnostinae Whitehouse, 1936
Genus *Han* gen. nov.

Derivation of name. After the Han Chinese.

Type and only known species. *Han solo* gen. et sp. nov.; lower Zitai Formation, Arenig Series, Maocaopu, Reshi, Taoyuan County, N Hunan, China.

Diagnosis. Pseudagnostine genus with glabellar node immediately anterior to F3. Cephalon subrectangular and pygidium subcircular to subquadrate; both cephalon and pygidium unconstricted; *en grande tenue*; non-scrobiculate. Median preglabellar furrow absent; glabellar anterolateral lobes meet sagittally, defined anteriorly and posteriorly by F3 and F2; anterior lobe small, subtrapezoidal. Pygidial axial node posteriorly defined; deuterolobe well defined by deep, plethoid accessory furrows; intranotular axis absent; terminal node present; non-retral posterolateral pygidial spines slightly anterior to posterior margin of deuterolobe (exsag.).

Remarks. In his revision of the Pseudagnostinae, Shergold (1977) considered 88 species which had been variously assigned to the closely related or synonymous genera and subgenera *Pseudagnostus* Jaekel, 1909, *Plethagnostus* Clark, 1923, *Rhaptagnostus* Whitehouse, 1936, *Sulcatagnostus* Kobayashi, 1937, *Pseudorhaptagnostus* Lermontova, 1940, *Euplethagnostus* Lermontova, 1940, *Neoagnostus* Kobayashi, 1955,

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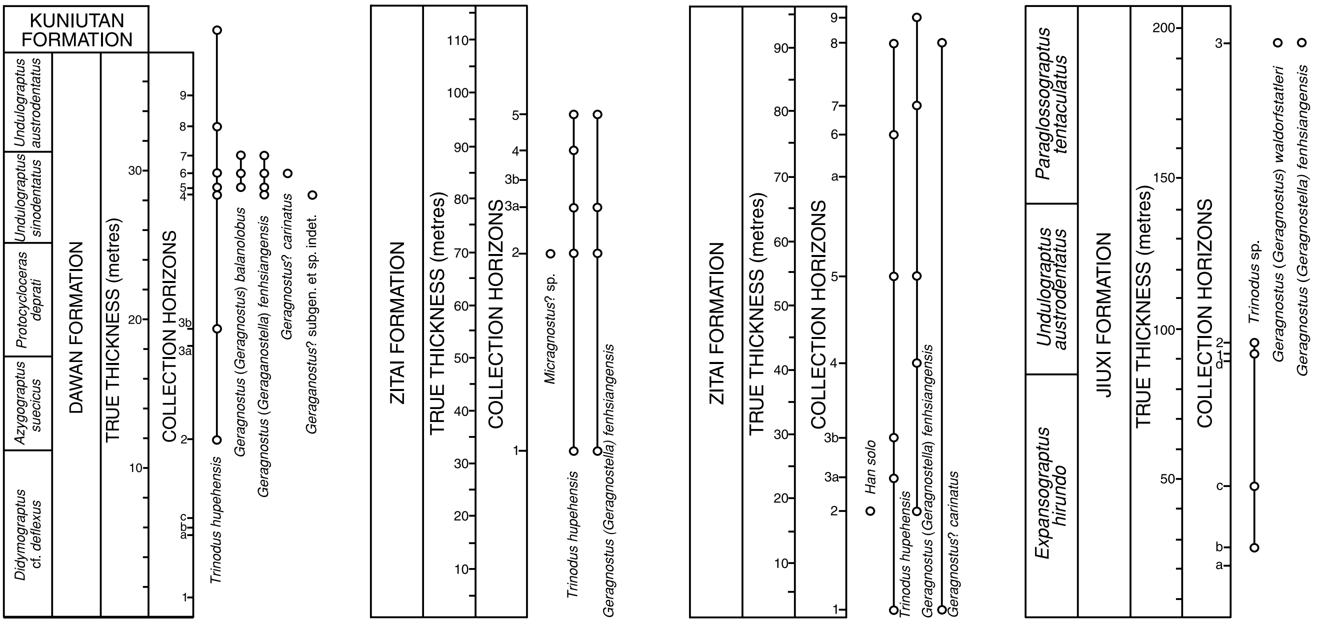

Figure 2 Vertical distribution of agnostid taxa against measured lithostratigraphic sections of (left to right) the Dawan and Kuniutan Formations at Daping, the Zitai Formation at Shuanghong, the Zitai Formation at Maocaopu, and the Jiuxi Formation at Baimaquan and Panjiazui. Modified from Turvey & Zhou (2002, 2004a); further information on collection horizon nomenclature in Turvey (2005a).

Hyperagnostus Kobayashi, 1955, *Machairagnostus* Harrington & Leanza, 1957 and *Pseudagnostina* Palmer, 1962. These were united by the possession of a deuterolobe similar to that of the type species of *Pseudagnostus*, *P. cyclopyge* (Tullberg, 1880), and were referred by Shergold (1977) to *Pseudagnostus sensu lato*. Shergold (1977) erected various species groups within *Pseudagnostus s.l.*, based primarily on the position of the axial glabellar node relative to the anterolateral glabellar lobes. According to Shergold (1977), species within *Pseudagnostus s.l.* fall broadly into two divisions: those in which the glabellar node is positioned posterior to F2, a condition referred to as spectaculate, and those in which the node interrupts the course of the glabellar furrows and lies between the anterolateral lobes, referred to as papilionate. Shergold (1977) assigned all of these species groups to the three genera *Pseudagnostus*, *Neoagnostus* and *Rhaptagnostus*; more recent authors have reinterpreted generic and subgeneric divisions and nomenclatural seniority within the group (Shergold *et al*. 1990; Nielsen 1997; Shergold & Laurie *in* Kaesler 1997).

Although the geological occurrence of *Pseudagnostus s.l.* is relatively long, it is a largely Cambrian group, with pseudoagnostines occurring from the *Proagnostus bulbus* Zone onwards (Resser 1938). Several pseudagnostine genera are present in Cambrian outer shelf facies of South China (Peng & Robison 2000). *Pseudagnostus s.l.* has previously only been recorded in the Ordovician from the Tremadoc (Shergold 1977); a thorough review of the stratigraphic occurrences and taxonomic placement of Ordovician pseudagnostines was provided by Nielsen (1997, 1999). The new Arenig pseudagnostine material from the Zitai Formation is thus markedly younger than any of the *Pseudagnostus s.l.* species considered by previous authors, and represents the youngest known member of the Diplagnostidae as a whole.

The single associated cephalon (Fig. 4c) displays a glabellar node positioned anterior to F3. This prevents straightforward assignment of the new material to any of Shergold's species groups. The anterior position of the glabellar node is consistent with Shergold (1977), who suggested that this character displayed an anteriorward migration during the evolution of the Pseudagnostinae (as determined by stratigraphic age), with papilionate forms being derived from spectaculate ones.

This character state suggests possible taxonomic affinity of the new species with the papilionate genus *Rhaptagnostus*, for which two possible Ordovician species were recognised by Nielsen (1997, 1999); however, this genus differs from the new species in several other cephalic and pygidial features, being partly to fully effaced, with nondeliquiate border furrows and minute pygidial marginal spines well in advance of the rear of the deuterolobe. On the basis of other characters, the new species appears to be more closely related to *Pseudorhaptagnostus* [=*Neoagnostus*; see Nielsen 1997, 1999 for discussion on seniority for this genus], for which both subgenera recognised by Nielsen (1997, 1999) and Shergold & Laurie *in* Kaesler (1997), *P.* (*Pseudorhaptagnostus*) [=*N.* (*Neoagnostus*) of Shergold & Laurie *in* Kaesler (1997)] and *P.* (*Machairagnostus*), occur in the Tremadoc. *P.* (*Machairagnostus*) differs from the new species in having a scrobiculate cephalon with a median preglabellar furrow, and a weakly deuterolobate pygidium which retains an intranotular axis. Within *P.* (*Pseudorhaptagnostus*), the new species is most similar to the *canadensis* species group of Shergold (1977), which differs in having fused anterior and anterolateral glabellar lobes; it is also quite similar to the *araneavelatus* species group in glabellar and pygidial axial morphology, although this species group tends to be considerably effaced. Both species groups also differ from the new species in having slightly constricted pygidial acrolobes.

Since the position of the glabellar node was used by Shergold (1977) to define generic-level differences within the Pseudagnostinae, and the overall morphology of the new species does not closely match that of other Ordovician representatives of the group, it is assigned to a new pseudagnostine genus. This morphology-based diagnosis is supported by the large stratigraphic interval between the occurrence of the new taxon in the Zitai Formation, and records of other Ordovician pseudagnostines from the Tremadoc.

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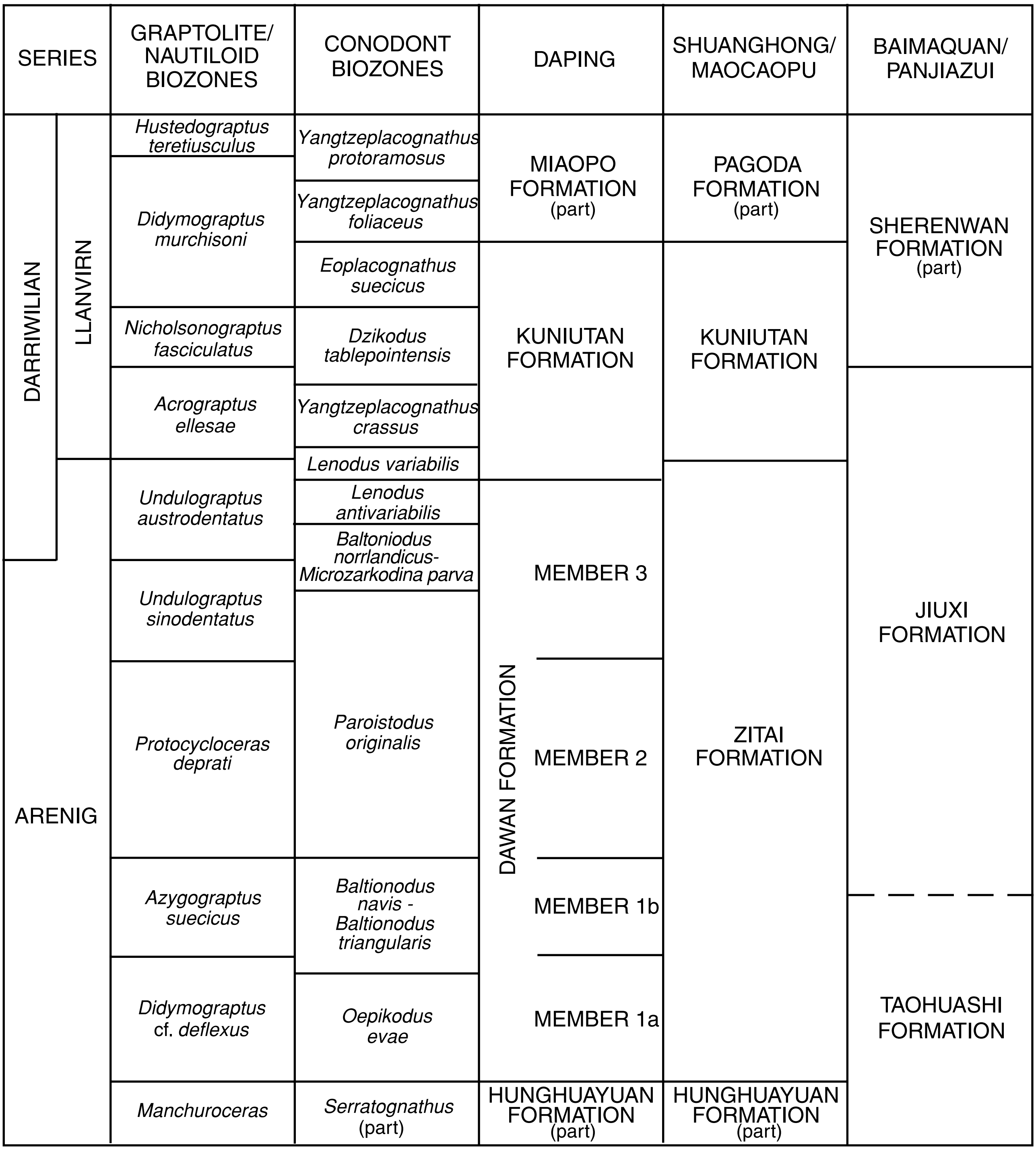


Figure 3 Correlation chart for the Arenig–Llanvirn stratigraphic units of W Hubei and N Hunan. From Turvey & Zhou (2004b).

Han solo gen. et sp. nov.
Figures 4c–e, i, 5

Derivation of name. Reflecting that this species appears to represent the last surviving member of the Diplagnostidae.

Holotype. Pygidium (NI 133788), Fig. 4e.

Type stratum and type locality. Bed 2, Zitai Formation, Arenig Series, Maocaopu, Reshi, Taoyuan County, N Hunan, China.

Paratypes. One cephalon (NI 133789) and two pygidia (NI 133791, 133890) from the type stratum and type locality.

Diagnosis. As for genus.

Description. Cephalon with maximum width (tr.), slightly anterior to cephalic midline (sag.), 85 per cent maximum length (sag.). Posterolateral spines present. Glabella occupies 60 per cent cephalic length (sag.) and 70 per cent acrolobe length. Basal lobes rounded subtriangular. Axial furrows approximately parallel for majority of their length, converging anteriorly to form rounded anterior glabellar margin. Posterior glabellar lobe convex (lat.). Anterolateral lobes subtriangular, occupying 50 per cent of glabella anterior to cephalic midline (sag); F2 anteriorly convex, chevronate; F3 posteriorly convex, shallow V-shape. Median glabellar node situated 75 per cent glabellar length from posterior glabellar margin. Acrolobe subquadrate; lateral fields parallel for posterior 50 per cent of acrolobe, with posterior margins level with anterior margin of basal lobes (exsag.). Border begins 25 per cent cephalic length from posterior cephalic margin;

anteriorly comprises less than 10 per cent cephalic length. Border furrow deliquiate, rather broad. Parietal surface smooth.

Pygidium with maximum width (tr.), at posterior tip of posterolateral spines, equal to or slightly longer than maximum length (sag.). Articulating facets diverge posteriorly at 80 degrees. Anteroaxis occupies 40 per cent acrolobe length (sag.); maximum width (tr.), at anterior margin of anteroaxis, 40 per cent maximum pygidial width and 50 per cent maximum acrolobe width. Axial furrows straight opposite anteroaxis, slightly convergent posteriorly. Anterolateral lobes subtrapezoidal, wider (tr.) than long; slightly wider (tr.) than median region of M1; abaxially flattened, adaxially subtriangular; well-defined posteriorly by slightly oblique F1; poorly defined adaxially by furrow oriented at 45 degrees; anterior margin slightly anteriorly convergent, disrupting articulating furrow. F1 effaced in median region of anteroaxis. M2 slightly longer (exsag.) than M1 at axial furrow, over twice as long sagittally. F2 complete, posteriorly convex in shallow V-shape. Axial node almost as long as adaxial margin of anterolateral lobes (exsag.); disrupts F2 slightly. Deuterolobe subtrapezoidal; plethoid accessory furrows straight, diverging posteriorly at almost 20 degrees; maximum width (tr.), at posterior edge of accessory furrow, 90 per cent maximum acrolobe width. Acrolobe subcircular to subquadrate. Flattened border slightly over 10 per cent pygidial length (sag.); posterolaterally slightly expanded; moderate spines extend posteriorly from position slightly anterior to posterior margin of deuterolobe (exsag.). Border furrow deliquiate, narrow. Parietal surface smooth.

Family Metagnostidae Jaekel, 1909

Remarks. The relationship between *Geragnostus* and *Trinodus* [=*Arthrorhachis*; see discussion under *Trinodus* for nomenclatural seniority for this genus] has been the source of considerable discussion in the literature (e.g. Fortey 1980; Ahlberg 1989a; Nielsen 1997, 1999). *Geragnostus* is currently used to define species with a pygidial posterolobe longer than the postaxial region of the pygidial acrolobe. The cephalon of *Trinodus* has a more subcircular acrolobe than that of *Geragnostus*; cephalic characters are generally regarded as insufficient to provide accurate differentiation between the two genera, although Nielsen (1997) established a subgenus of *Geragnostus*, *G.* (*Novoagnostus*), to describe material with *Geragnostus*-type pygidia and *Trinodus*-type cephala. However, several metagnostid species known from substantial material display considerable intraspecific variation in posterolobe morphology and length (e.g. *Geragnostus clusus* Whittington, 1963: pl. 1, figs 4, 11, 14; *G. nesossii* Harrington & Leanza, 1957: fig. 9, 1–5; in addition to species listed by Nielsen 1997). Many species were not immediately assignable by Nielsen (1997) to the diagnoses of *Geragnostus* or *Trinodus*, and were left in open nomenclature; it is possible that further work on these species may lead to revision of the taxonomic delimitation between the two genera. Alternative species-groupings to those used by Nielsen (1997), such as uniting species of *Geragnostus* with subquadratic posterolobes, e.g. *Geragnostus sidenbladhi* (Linnarsson, 1869), may also prove taxonomically significant.

Genus *Trinodus* M'Coy, 1846

Type species. *Trinodus agnostiformis* M'Coy, 1846; Campile Formation, Upper Harnagian–Soudleyan substages, Burrellian Stage, Caradoc Series, Greenville, Enniscorthy, County Wexford, Ireland. By monotypy.

Remarks. The type species of *Trinodus*, *T. agnostiformis*, was until recently only known from a single cephalon, figured by M'Coy (1846: pl. 4, fig. 3), Whittington (1950: pl. 68, figs 1–3) and Owen & Parkes (2000: text-fig. 3a–b). Additional material from the type locality was apparently unknown, although M'Coy (1846) reported that the species was 'not uncommon'. A large number of Ordovician species have been assigned to *Trinodus* in the literature (Nielsen 1997, 1999), but as the characters used for distinguishing between this genus and *Geragnostus* are pygidial rather than cephalic, Fortey (1980) restricted the use of *Trinodus* to the type specimen. Species displaying short pygidial posterolobes were reallocated by Fortey (1980) to *Arthrorhachis*, as pygidial material is known for its type species, *A. tarda* (Barrande, 1846). This approach was largely followed by subsequent authors (e.g. Shergold *et al*. 1990; Shergold & Laurie *in* Kaesler 1997; Nielsen 1997, 1999), although Zhou (1987) regarded reallocation as a temporary measure. Pygidia assignable to *T. agnostiformis* have recently been collected from the type locality (Owen & Parkes 2000: text-fig. 3c, e), and the lectotype pygidium of *Agnostus trinodus* Salter, 1848, probably also from Greenville, was also considered by Owen & Parkes (2000; see text-fig. 3d) to represent *T. agnostiformis*. Although all of these pygidia are either distorted or incompletely preserved, they are very similar to the pygidium of *A. tarda*, which led Owen & Parkes (2000) to reinstate *Trinodus* as the senior synonym of *Arthrorhachis*. This approach is followed herein, although *Arthrorhachis* has been retained as a distinct genus by other recent authors (Peng *et al*. 2001).

Trinodus hupehensis Lu, 1975
Figure 4f–h, j–l, p

1975 *Trinodus hupehensis* Lu; p. 93 (297), pl. 1, figs 12–15.
1977 *Trinodus hupehensis* Lu; Zhou *et al*., p. 110, pl. 36, figs 18–19.
1984 *Trinodus hupehensis* Lu; Sun, p. 331, pl. 146, figs 4–6.
1985 *Trinodus hupehensis* Lu; Duan, p. 123, pl. 1, figs 1–2, 12.
1987 *Arthrorhachis hupehensis* (Lu); Fortey & Owens, p. 115.
1987 *Arthrorhachis hupehensis* (Lu); Zhou, p. 656.
1999 *Arthrorhachis hupehensis* (Lu); Nielsen, p. 95.
2002 *Trinodus hupehensis* Lu; Turvey & Zhou, pl. 1, fig. 5.
2005a *Trinodus hupehensis* Lu; Turvey, pl. 2, fig. 3.

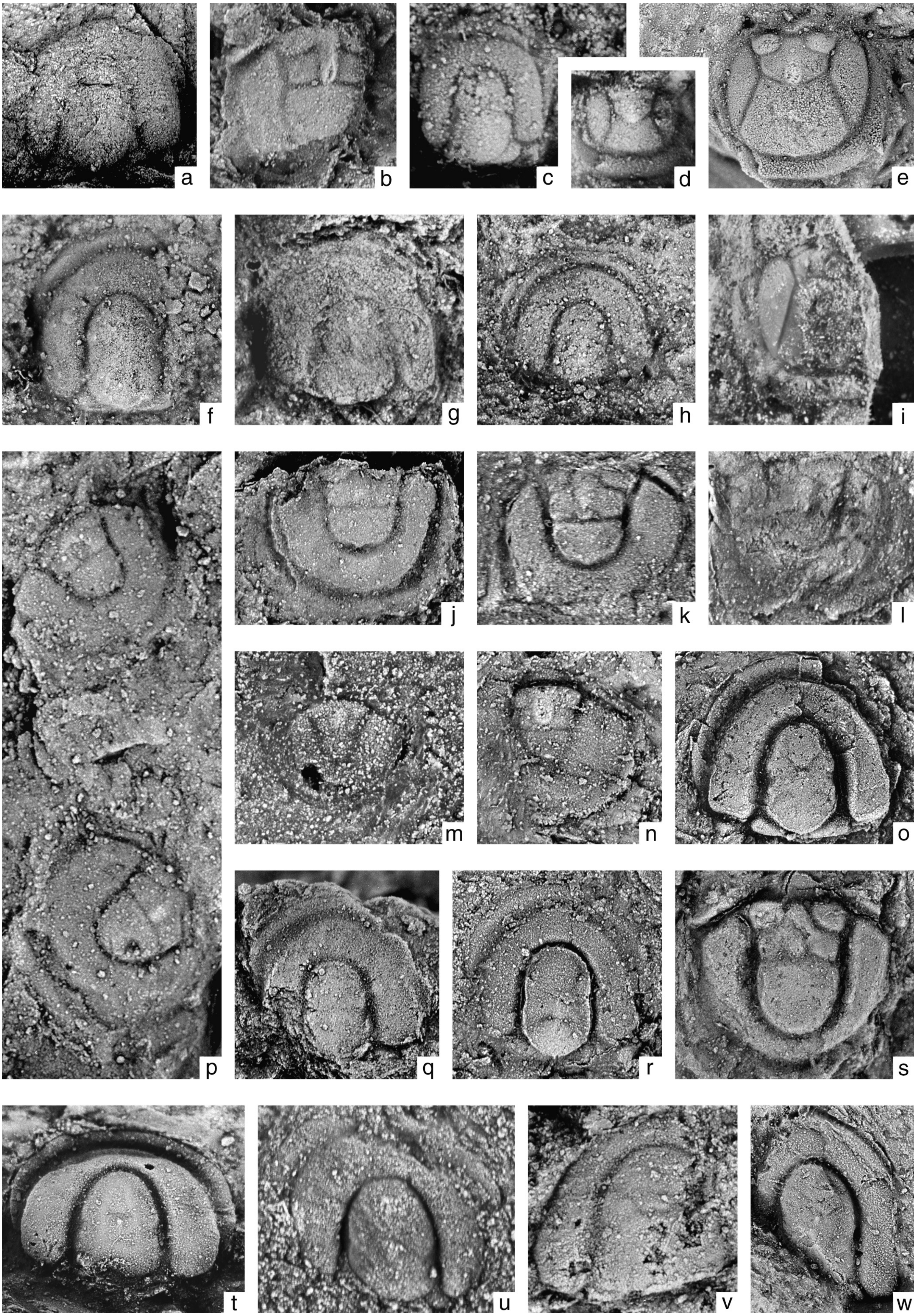
Holotype. Cephalon (NI 16373); figured Lu (1975: pl. 1, fig. 12); refigured Sun (1984: pl. 146, fig. 4).

Type stratum and type locality. Member 3, Dawan Formation, upper Arenig Series, Miaopu, Fenxiang, Yichang County, W Hubei, China.

Material. Two pygidia (NI 133776, 133795) from Bed 4 of the Dawan Formation at Daping; one pygidium (NI 133797) from Bed 5 of the Dawan Formation at Daping; two pygidia (NI 133796) from Bed 6 of the Dawan Formation at Daping; two cephala (NI 133792–133793) from the base of the Kuniutan Formation at Daping; one cephalon (NI 133794) from Bed 1 of the Zitai Formation at Shuanghong.

Diagnosis. Species of *Trinodus* with subcircular to subquadrate cephalon and pygidium; pygidial axis occupies 50 per cent pygidial length; pygidial anterolateral lobes rectangular, slightly wider (tr.) than median region of M1; M2 slightly longer (sag.) than M1; posterolobe rounded subrectangular, almost as wide (tr.) as anteroaxis; terminal node present, giving posterior margin of posterolobe a 'pinched' appearance; pygidial acrolobe subcircular to subquadrate, broadly convex.

Description. Cephalon with maximum width (tr.), at cephalic midline (sag.), approximately equal to maximum



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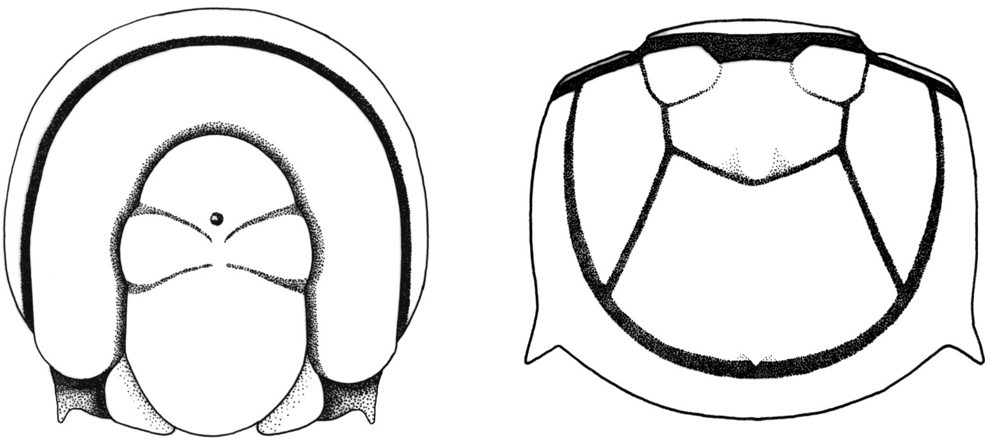

Figure 5 Reconstruction of the external exoskeletal surface of the cephalon and pygidium of *Han solo* gen. et sp. nov., × 25.

length (sag.). Posterior border furrow, occipital furrow and axial furrows *en grande tenue*. Tiny posterolateral spines present. Glabella occupies 61–64 per cent cephalic length (sag.), and over 70 per cent acrolobe length. Maximum glabellar width excluding basal lobes (tr.), level with anterior margin of basal lobes, 35 per cent maximum cephalic width (tr.); maximum glabellar width including basal lobes, at posterior glabellar margin, up to 40 per cent maximum cephalic width. Basal lobes short (exsag.), rounded subtriangular. Axial furrows approximately parallel for posterior 65 per cent of their length, defining F2 with slight adaxial notch at glabellar midlength (exsag.); converging opposite anterior 35 per cent of glabella, to produce a rounded trapezoid or convex angular anterior glabellar margin. Glabellar surface largely effaced both externally and parietally. Acrolobe subovoid to subquadrate; lateral fields evenly rounded posterolaterally, and subparallel for posterior 50 per cent of cephalon. Flattened border present around anterior 65 per cent of cephalon; 10 per cent cephalic length at anterior margin (sag.). Border furrow well-defined and deliquiate on parietal surface, occupying 50 per cent of border; almost absent on external surface. External and parietal surfaces smooth.

Pygidium with maximum width (tr.), at posterior edge of articulating facet, approximately equal to maximum length (sag.). Pygidial furrows *en grande tenue*. Half-ring transverse. Ridge-like shoulders of articulating facet diverge posteriorly at 60 degrees. Axis (excluding half-ring) occupies almost 65 per cent acrolobe length (sag.); maximum axial width (tr.) at anterior margin of anteroaxis, almost 40 per cent maximum pygidial width and 50 per cent maximum acrolobe width. Anteroaxis and posterolobe of equal length (sag.). Axial furrows straight and slightly posteriorly convergent at 10 degrees opposite M1, subparallel to slightly posteriorly convergent opposite M2 and most of posterolobe. Anterolateral lobes wider (tr.) than long, well defined by slightly anteriorly convergent furrows adaxially and slightly oblique F1 posteriorly. F1 effaced in median region of anteroaxis. F2 transverse. Axial node present across most of median region of M2, slightly more heavily defined posteriorly; does not disrupt F2. Posterolobe wider (tr.) than long (sag.); approximately equal in length (sag.) to postaxial region of acrolobe. Flattened border 10 per cent pygidial length (sag.) and maximum width (tr.); posterolaterally expanded, to almost twice posterior width in some specimens, with small posterolateral spines present at level of posterior margin of acrolobe (exsag.). Border furrow absent externally; deliquiate and broad, of at least equal width to border and slightly posterolaterally expanded parietally. External and parietal surfaces smooth.

Remarks. Nielsen (1997) considered *Trinodus*, then referred to *Arthrorhachis*, to contain many synonymous species. However, Fortey & Owens (1987) regarded *T. hupehensis* as a distinctive species, as one of the pygidia figured by Lu (1975: pl. 1, fig. 13) has an axis with a posterolobe wider than M2. This character aligns it only with *A.* sp. indet. of Fortey & Owens (1987: p. 114, fig. 16) from the upper Arenig (Fennian Stage) of S Wales, which differs from *T. hupehensis* in having a narrower pygidial border, and a considerably shorter, more subquadratic posterolobe. However, both of the other paratype pygidia of *T. hupehensis* (Lu 1975: pl. 1, figs 14–15) and newly collected pygidia referable to the species (Fig. 4j–l, p) display a posterolobe which, although broader than is typical for the genus, is approximately the same width as or slightly narrower than M2, with axial furrows which converge posteriorly slightly for the majority of the length of the posterolobe.

Nielsen (1997, 1999) placed *T. hupehensis* into his *elspethi* species group on the basis of its relatively long posterolobe. This character state is shown clearly in new pygidia, as is the parietally expressed wide pygidial border used by Fortey & Owens (1987) as a diagnostic character of the species.

Trinodus sp.
Figure 4m–n

2004a *Trinodus* sp.; Turvey & Zhou, fig. 7b.

Figure 4 (a–b) *Micragnostus*? sp.: Bed 2, Shuanghong: (a) cephalon, NI 133786, × 15; (b) pygidium, NI 133787, × 15. (c–e, i) *Han solo* gen. et sp. nov., Bed 2, Maocaopu: (c) cephalon, NI 133789, × 25; (d) pygidium, NI 133890, × 20; (e) pygidium (holotype), NI 133788, × 15; (i) latex cast of pygidium, NI 133791, × 12. (f–h, j–l, p) *Trinodus hupehensis* Lu, 1975: (f) cephalon, NI 133792, × 12, base of Kuniutan Formation, Daping; (g) cephalon, NI 133794, × 15, Bed 1, Shuanghong; (h) cephalon, NI 133793, × 20, base of Kuniutan Formation, Daping; (j) pygidium, NI 133795, × 15, Bed 4, Daping; (k) pygidium, NI 133776, × 20, Bed 4, Daping; (l) pygidium, NI 133797, × 16, Bed 5, Daping; (p) two pygidia, NI 133796, × 15, Bed 6, Daping. (m-n) *Trinodus* sp.: (m) pygidium, NI 133979, × 25, Bed 2, Panjiazui; (n) pygidium, NI 133978, × 20, Bed 1, Panjiazui. (o, q–s) *Geragnostus* (*Geragnostus*) *balanolobus* sp. nov.: (o) cephalon, NI 133801, × 12, Bed 7, Daping; (q) cephalon, NI 133803, × 16, Bed 7, Daping; (r), cephalon, NI 133802, × 16, Bed 6, Daping; (s) pygidium (holotype), NI 133800, × 15, Bed 7, Daping. (t-w) *Geragnostus* (*Geragnostus*) *waldorfstatleri* sp. nov.: Bed 3, Panjiazui; (t) cephalon, NI 133805, × 15; (u) cephalon, NI 133808, × 12; (v) cephalon, NI 133806, × 15; (w) cephalon, NI 133807, × 10.

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Material. One pygidium (NI 133978) from Bed 1 of the Jiuxi Formation at Panjiazui; one pygidium (NI 133799) from Bed 2 of the Jiuxi Formation at Panjiazui.

Remarks. Incompletely preserved metagnostid material from Panjiazui is assignable to *Trinodus* on the basis of its short pygidial posterolobe. It clearly differs from *T. hupehensis* in having a subtriangular pygidial axis and a subovoid posterolobe which occupies only 25 per cent pygidial width, and in apparently lacking a terminal node. It probably represents a new species; however, the material is insufficient to warrant erection of a new specific name, and so is left under open nomenclature herein.

Genus *Geragnostus* Howell, 1935
Subgenus *Geragnostus* (*Geragnostus*) Howell, 1935

Type species. *Agnostus sidenbladhi* Linnarsson, 1869; Bjørkåsholmen Formation, Tremadoc Stage, Västergötland, Sweden. By original designation.

Geragnostus (*Geragnostus*) *balanolobus* sp. nov.
Figures 4o, q–s, 6

1984 *Geragnostus fenhsiangensis* Lu; Sun, pl. 146, fig. 3.
1997 *Geragnostus* (*Novoagnostus*) sp.?; Nielsen, p. 486.
1999 *Geragnostus* (*Novoagnostus*) sp.?; Nielsen, p. 82.

Derivation of name. Greek '*balanos*', acorn, and '*lobos*', lobe, referring to the shape of the pygidial posterolobe.

Holotype. Pygidium (NI 133800), Fig. 4s; Bed 7, *Undulograptus sinodentatus* Biozone, Dawan Formation, upper Arenig Series, Daping, Yichang County, W Hubei, China.

Paratypes. One cephalon (NI 133802) from Bed 6 of the Dawan Formation at Daping; two cephala (NI 133801, 133803) from Bed 7 of the Dawan Formation at Daping.

Diagnosis. Species of *Geragnostus* (*Geragnostus*) with subovoid cephalon and cephalic acrolobe and subcircular pygidium; anterolateral lobes of pygidium wider (tr.) than median region of M1; M1 slightly shorter (sag. and exsag.) than M2; pygidial posterolobe large, glandiform, slightly expanded relative to M2, longer (sag.) than anteroaxis and extending almost 85 per cent distance to posterior border furrow; axial furrows very deep and broad; pygidial acrolobe narrow (tr.) and subcircular, with rounded border furrows.

Description. Cephalon with maximum width (tr.), at 35 per cent cephalic length from posterior cephalic margin, slightly greater than maximum length (sag.). Posterior border furrow, occipital furrow and axial furrows *en grande tenue*. Posterior border furrow broad and deep; occipital furrow deep, slightly narrower. Posterolateral spines small. Glabella occupies 55–60 per cent cephalic length (sag.), and 75 per cent acrolobe length. Maximum glabellar width excluding basal lobes (tr.), level with anterior margin of basal lobes, 35 per cent maximum cephalic width (tr.); maximum glabellar width including basal lobes, at posterior margin of glabella, 40 per cent maximum cephalic width. Basal lobes short (exsag.) and asymmetrical, extending further adaxially than abaxially, reaching cephalic midline (tr.) and fusing at base of glabella. Axial furrows approximately parallel for at least posterior 50 per cent of their length (exsag.); converging opposite anterior 35–50 per cent of glabella to produce an anterior glabellar margin which varies from trapezoid or convex angular to fairly evenly rounded. External exoskeletal surface of glabella largely effaced. F1 present at 25–35 per cent glabellar length from posterior glabellar margin; expressed either as faint transverse furrow, curving forwards slightly towards glabellar midline, or as a pair of faint depressions oriented slightly obliquely, situated 50 per cent distance between glabellar midline (tr.) and axial furrows. F2 expressed as slight constriction in axial furrows at glabellar midlength (exsag.). Glabellar node expressed as faint median swelling opposite F2. F3 faintly visible 65 per cent glabellar length from posterior margin; slightly anteriorly convex, with lateral extensions curving anteriorly for almost 50 per cent remaining distance to anterior margin. Flattened border 10 per cent cephalic length (sag.) and maximum width (tr.); well-defined border furrow deliquiate and broad, occupying 50 per cent of border. Parietal surface smooth.

Pygidium with maximum width (tr.), at posterior edge of articulating facet, approximately equal to maximum length (sag.). Half-ring transverse for most of its length, slightly narrower than M1, separated from anteroaxis by wide, transverse articulating furrow; half-ring and furrow together make up almost 20 per cent of axial length (sag.). Articulating facet defined posteriorly by ridge-like anterior shoulders, which diverge posteriorly at 60 degrees. Axis (including half-ring) occupies 75 per cent pygidial length (sag.), and 85 per cent acrolobe length; maximum axial width (tr.) at anterior margin of anteroaxis, almost 40 per cent maximum pygidial width and 50 per cent maximum acrolobe width. Axial furrows *en grande tenue*, heavily emphasised, straight and slightly convergent posteriorly at 10 degrees opposite anteroaxis, diverging slightly posteriorly to describe tumescent, subovoid posterolobe. Anterolateral lobes tetragonal, well defined by anterolaterally oblique furrows adaxially and slightly oblique F1 posteriorly. F1 effaced medially. F2 transverse. Axial node defined posteriorly in M2, extends posteriorly to slightly disrupt F2. Terminal node absent. Pleural fields narrower opposite rounded postaxial margin than opposite anteroaxis. Flattened border 10 per cent pygidial length (sag.) and maximum width (tr.); expanded slightly opposite posterior margin of posterolobe into short posterolateral spines. Well-defined border furrow deliquiate and broad, occupying at least 50 per cent of border. Parietal surface smooth.

Remarks. Material assignable to *G.* (*Geragnostus*) from Daping is not conspecific with any of the Arenig taxa assigned to the subgenus by Nielsen (1997, 1999), as it displays a long, glandiform pygidial posterolobe, and is referred to a new species, *G.* (*G.*) *balanolobus*. An agnostid pygidium from the Dawan Formation of Fenxiang, Yichang County, figured by Sun (1984: pl. 146, fig. 3) as *Geragnostus fenhsiangensis*, is very similar to the new species and is interpreted as conspecific. Although Nielsen (1997, 1999) considered that this pygidium might be assignable to *G.* (*Novoagnostus*) Nielsen, 1997, the length of the posterolobe is more typical of *G.* (*Geragnostus*).

The new species shows some similarity to *G.* (*G.*) *crassus* Tjernvik, 1956, from the Tremadoc of Baltica; this species differs in having a wider, rounded or swollen rather than glandiform posterolobe (see Ahlberg 1992 for a revision of *G.* (*G.*) *crassus*). Pygidia referred to *G.* sp. (cf. *G. crassus* Tjernvik) from the Tremadoc of Yingou, Yumen County, Gansu (Chang & Fan 1960: pl. 1, figs 2–3; Lu *et al*. 1965: pl. 2, figs 1–2), and *G. crassus*? from the lower Llanvirn of Angzhanggou, also in Yumen County (Chang & Fan 1960: pl. 1, fig. 4; Lu *et al*. 1965: pl. 2, fig. 5), differ from the new species in having more subquadratic posterolobes which do not extend as far posteriorly. *G.* (*G.*) *splendens* (Holub, 1912) and *G.* (*G.*) cf. *splendens* of Ahlberg (1992: p. 553, figs 10k–o, 11a–i), from the Arenig of Bohemia and Baltica respectively, are cephalically similar to the new species, but also have wider and shorter subquadratic posterolobes. *G. carinatus*, the only South Chinese Arenig metagnostid assigned to the subgenus by Nielsen (1997, 1999), has been incorrectly interpreted by

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previous authors (see below); its glabella differs from that of the new species in displaying a faint posterior median keel.

Geragnostus (*Geragnostus*) *waldorfstatleri* sp. nov.
Figures 4t–w, 7a–c, 8

2004a *Geragnostus* (*Geragnostus*) sp. nov.; Turvey & Zhou, figs 7a, e.

Derivation of name. After the resemblance of the pygidial axis to the heads of Waldorf and Statler, two characters from 'The Muppet Show'.

Holotype. Pygidium (NI 133804), Fig. 7b; Bed 3, *Amplexograptus confertus* Biozone, Jiuxi Formation, lower Llanvirn Series, Panjiazui, Taoyuan County, N Hunan, China.

Paratypes. Four cephala (NI 133805–133808) and two pygidia (NI 133809–133810) from Bed 3 at Panjiazui.

Diagnosis. Species of *Geragnostus* (*Geragnostus*) with subovoid cephalon and pygidium; pygidial axis 75 per cent pygidial length (sag.); anterolateral lobes of pygidium of equal anterior width (tr.) to median region of M1; pygidial posterolobe palate, long (sag.) and with anterior two-thirds almost parallel-sided, over 35 per cent pygidial length and extending over 80 per cent distance to posterior border furrow; axial furrows deep but quite narrow; pygidial acrolobe narrow, subovoid, with evenly convergent border furrows.

Description. Cephalon with maximum width (tr.), at posterior cephalic margin, greater than maximum length (sag.). Posterior border furrow and axial furrows *en grande tenue*. Glabella occupies 60 per cent or more cephalic length (sag.) and 75 per cent acrolobe length. Maximum glabellar width excluding basal lobes (tr.), opposite anterior margin of basal lobes, 40 per cent maximum cephalic width (tr.); maximum glabellar width including basal lobes, at posterior margin of glabella, 50 per cent maximum cephalic width. Basal lobes small and asymmetrical, sloping further adaxially than abaxially. Glabella parallel-sided for 65 per cent length (sag.); axial furrows remain straight but converge anteriorly; anterior glabellar furrow transverse, giving anterior glabellar margin a convex trapezoid outline in flattened material; margin more rounded in unflattened material. External exoskeletal surface of glabella largely effaced. Median glabellar node present at glabellar midlength (sag.) of parietal surface. Faint, slightly convex F3 present on parietal surface, 65 per cent glabellar length from posterior axial margin (sag.); median region transverse, lateral extensions anteriorly convex, extending anteriorly for 50 per cent remaining distance to anterior margin. Acrolobe convex-subrectangular to subovoid. Border wide and flattened anteriorly, occupying 10 per cent cephalic length (sag.). Border furrow quite broad and well-defined on parietal surface. Parietal and external surfaces smooth.

Pygidium with maximum width (tr.), at posterior edge of articulating facet, equal to maximum pygidial length (sag., excluding half-ring). Pygidial furrows *en grande tenue*. Half-ring short (sag.), anteriorly convex, with straight (tr.) posterior margin; articulating furrow quite long (sag.) and deep. Anterior shoulders of articulating facet diverge posteriorly at 60 degrees. Maximum axial width (tr.) at anterior margin of anteroaxis, over 35 per cent maximum pygidial width and 40–50 per cent maximum acrolobe width. Anteroaxis shorter (sag.) than posterolobe; occupies 35 per cent pygidial length (excluding half-ring). Axial furrows converge evenly at 10 degrees opposite anteroaxis. Anterolateral lobes tetragonal, defined by straight parasagittally oriented furrows adaxially and posterolaterally oriented F1 posteriorly; anterior margins very slightly anteriorly convex. M1 and M2 equal in length (exsag.) at axial furrows; median region of M2 twice as long (sag.) as that of M1. Axial node defined posteriorly, occupying 35 per cent length (sag.) of anteroaxis; slightly narrower (tr.) than median region of M1. F2 transverse. Axial furrows almost straight opposite posterior lobe, converging quite abruptly in posterior 35 per cent of lobe to form angled posterior termination. Terminal node absent. Acrolobe not very adaxially convex, converging posteriorly rather abruptly to a rounded, narrow (tr.) postaxial margin. Border evenly rounded, wide and flattened, occupying 10 per cent pygidial length (sag.). Border furrow deliquiate and broad, well-defined laterally, becoming slightly shallower posteriorly. Posterolateral spines apparently absent. Parietal surface smooth.

Remarks. This new species from Panjiazui is morphologically distinct from any of the Arenig or Llanvirn representatives of *G.* (*Geragnostus*) listed by Nielsen (1997, 1999), being distinguished primarily by a long, almost parallel-sided pygidial posterolobe with a terminal point rather than a rounded posterior margin, shaped much like the head of a spade. It is somewhat similar to a specimen of *G. clusus* Whittington, 1963 (pl. 1, figs 10, 11), from the Llanvirn of Lower Head, Newfoundland, which displays a laterally and posteriorly expanded posterolobe, but all individuals of the latter species have much narrower median M1 regions, and more rounded pygidial posterolobes and acrolobes. It is also similar to a pygidium from Nevada, left in open nomenclature by Ross (1970: pl. 10, figs 4–9), which differs from the new species in having a distinct notch in the pygidial axial furrow opposite F2, a more rounded posterolobe and a less posteriorly convergent acrolobe.

Subgenus *Geragnostus* (*Geragnostella*) Kobayashi, 1939

Type species. *Agnostus tullbergi* Novák, 1883; Šárka Formation, Llanvirn Series, Osek, near Rokycany, Czech Republic. By original designation.

Remarks. Kobayashi (1939) erected *Geragnostella* as a subgenus of *Geragnostus*, to describe species with a prominent pygidial node and effaced furrows opposite the pygidial posterolobe. Some authors (e.g. Whittard 1955; Lu 1975) have since raised *Geragnostella* to the level of separate genus, but more commonly it has been interpreted as a junior synonym of *Geragnostus* (see Nielsen 1997), as the characters used to define *Geragnostella* have been considered to be of low taxonomic significance. Shergold *et al.* (1990) and Shergold & Laurie *in* Kaesler (1997) reinstated *Geragnostella* as a valid genus. Nielsen (1997, 1999) also viewed *Geragnostella* as a valid taxon, although his reconsideration of the distribution of morphological characters within Ordovician agnostids led him to regard it as better interpreted as a subgenus of *Geragnostus*. His approach is followed herein, although Nielsen (1997) himself considered that, although intermediate forms between *Geragnostus* and *Geragnostella* do not seem to occur, both *Geragnostella* and another taxon he interpreted as a subgenus of *Geragnostus*, *Neptunagnostella* Pek, 1977, may not represent valid natural groups.

Geragnostus (*Geragnostella*) *fenhsiangensis* Lu, 1975
Figure 7d–o

non 1960 *Geragnostus* sp. (cf. *G. wimani* Tjernvik, 1956); Chang & Fan, p. 99, pl. 1, fig. 5 [=*Geragnostus* (*Geragnostus*) sp.].

1975 *Geragnostus fenhsiangensis*; Lu, p. 92 (278), pl. 1, figs 9–10.

? 1975 ?*Geragnostella* sp.; Lu, p. 92 (279), pl. 1, fig. 11.

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1977 *Geragnostus fenhsiangensis* Lu; Zhou *et al.,* p. 109, pl. 36, figs 14–15.
1984 *Geragnostus fenhsiangensis* Lu; Sun, p. 331, pl. 146, figs 1–2 (*non* fig. 3 [=*Geragnostus* (*Geragnostus*) *balanolobus*]).
1987 *Geragnostus fenhsiangensis* Lu; Zhou, p. 657.
1990 *Micragnostus* (*Anglagnostus*) *fenhsiangensis* (Lu); Peng, p. 72.
1999 *Geragnostus* (*Geragnostella*) *fenhsiangensis* Lu; Nielsen, p. 81.
2004a *Geragnostus* (*Geragnostella*) *fenhsiangensis* Lu; Turvey & Zhou, figs 6a, d.
2005a *Geragnostus* (*Geragnostella*) *fenhsiangensis* Lu; Turvey, pl. 2, figs 1–2.

Holotype. Cephalon (NI 16370); figured Lu (1975: pl. 1, fig. 9); refigured Sun (1984: pl. 146, fig. 1). *Non* cephalon (XI Tr002), cited as holotype by Zhou (1987).

Type stratum and type locality. Member 3, Dawan Formation, upper Arenig Series, Fenxiang, Yichang County, W Hubei, China.

Material. One pygidium (NI 133818) from Bed 5 of the Dawan Formation at Daping; three cephala (NI 133812–133813, 134043) and one pygidium (NI 133816) from Bed 6 of the Dawan Formation at Daping; two cephala (NI 133814–133815) from Bed 7 of the Dawan Formation at Daping; one thoracopygon (NI 133820) from Bed 1 of the Zitai Formation at Shuanghong; one cephalon (NI 133870) and one pygidium (133817) from Bed 2 of the Zitai Formation at Maocaopu; two pygidia (NI 133811, 134084) from Bed 3 of the Jiuxi Formation at Panjiazui.

Diagnosis. Species of *Geragnostus* (*Geragnostella*) with subquadrate cephalon and pygidium; glabella slightly conical, largely effaced; cephalic acrolobe subovoid; pygidial axis occupies 65 per cent pygidial length; pygidial anterolateral lobes square, of equal width (tr.) to median region of M1; M1 and M2 equal in length (sag.); pygidial posterolobe palate or subtriangular, poorly defined, occupying over 35 per cent pygidial length (sag.); terminal node clearly defined on parietal surface; pygidial acrolobe subovoid, gently convex; border furrows faint on external surface, but deliquiate and broad on parietal surface, occupying at least 50 per cent of border.

Description. Cephalon with maximum width (tr.), at cephalic midline (sag.), approximately equal to maximum length (sag.). Posterior border furrow, occipital furrow and axial furrows *en grande tenue*. Posterior border furrow broad and deep; occipital furrow narrower and shallower. Tiny posterolateral spines present, 50 per cent distance between lateral margin and abaxial margin of basal lobes. Glabella occupies 65 per cent cephalic length (sag.) and 75 per cent acrolobe length. Maximum glabellar width excluding basal lobes (tr.), opposite anterior margin of basal lobes, slightly over 35 per cent maximum cephalic width (tr.); maximum glabellar width including basal lobes, at posterior margin of glabella, 40 per cent maximum cephalic width. Basal lobes very short (exsag.) and flattened, reaching cephalic midline (tr.) and fusing at base of glabella as very short (sag.) occipital ring. Axial furrows subparallel in unflattened specimens; posterior part of axis higher (lat.) than anterior part, so appears wider (tr.) in flattened specimens; converging anteriorly more strongly opposite F3, with anterior glabellar margin rounded. Median glabellar node expressed on parietal surface at glabellar midlength (sag.). F2 expressed as slight constriction in axial furrows immediately anterior to glabellar node (exsag.). F3 faintly visible 65 per cent glabellar length from posterior margin; median region transverse, lateral extensions diverging anteriorly at 45 degrees for 50 per cent remaining distance to anterior glabellar margin. Flattened border begins at 25 per cent cephalic length from posterior cephalic margin; slightly expanded anterolaterally; anteriorly occupies 10 per cent cephalic length (sag.). Parietal and external surfaces smooth.

Thoracic axial region slightly wider (tr.) than maximum width of pygidial axis. Median lobe of first thoracic segment rounded, expanded at posterior margin. Lateral lobes rounded subtriangular, narrower anteriorly. First pleura apparently equal width (tr.) to lateral lobes; with strong pleural furrow, and raised nodes expressed on both anterior and posterior bands. Second thoracic segment slightly over 50 per cent length (sag.) of first segment (excluding half-ring). Median lobe of second thoracic segment subrectangular, anterior margin slightly narrower (tr.) than posterior margin; twice as wide (tr.) as long (sag.). Lateral lobes subovoid, slightly narrower (tr.) than median lobe. Second pleura equal width (tr.) to median lobe, and almost twice width of first pleura; with broad, blunt triangular termination; anterior band distinct; posterior band only expressed adaxially, as rounded swelling.

Pygidium with maximum width (tr.), at 35 per cent pygidial length from anterior margin, approximately equal to maximum length (sag.). Half-ring short (sag.), with transverse posterior margin; articulating furrow short but quite deep. Anterior shoulders of articulating facet diverge posteriorly at 70 degrees. Maximum axial width (tr.) at anterior margin of anteroaxis, equal to almost 40 per cent maximum pygidial width and almost 50 per cent maximum acrolobe width. Anteroaxis slightly shorter than posterolobe (sag.). Axial furrows well defined opposite anteroaxis, straight and converging posteriorly at 10 degrees. Anterolateral lobes defined by parasagittally oriented furrows adaxially and slightly oblique, slightly posteriorly convex F1 posteriorly. F1 effaced in median region of anteroaxis. Axial node large and well-defined across entire median region of M2; does not disrupt F2 posteriorly. F2 fairly well-defined, slightly anteriorly convex. Abaxially convex axial furrows converge gently posteriorly to produce a slightly angled posterolobe posterior margin. Flattened border slightly less than 10 per cent pygidial length (sag.) and maximum width (tr.); posterolaterally expanded, to almost twice posterior width in some specimens, with extremely small posterolateral spines present slightly anterior to level of posterior margin of acrolobe (exsag.). Parietal and external surfaces smooth.

Remarks. *G. fenhsiangensis*, recorded from the *Undulograptus austrodentatus* Biozone of the Dawan Formation by Lu (1975), was assigned to *G.* (*Geragnostella*) by Nielsen (1997). A pygidium identified as ?*Geragnostella* sp. by Lu (1975: pl. 1, fig. 11), from the older *Azygograptus suecicus* Biozone of the Dawan Formation, displays a slightly broader posterolobe than the pygidium of *G.* (*Geragnostella*) *fenhsiangensis* figured by Lu (1975), but is otherwise very similar and is probably conspecific. Lu (1975) also included the pygidium figured as *Geragnostus* sp. (cf. *G. wimani* Tjernvik, 1956) by Chang & Fan (1960, pl. 1, fig. 5), from the upper Arenig of the Qilian Mountains, Oulongbuluke, NE Qaidam, Qinghai, within *G.* (*Geragnostella*) *fenhsiangensis*. This was followed by Zhou (1987), but Nielsen (1997) reinterpreted this specimen as representing *G.* (*Geragnostus*) due to its uneffaced, deep pygidial axial furrow and apparent lack of a terminal node, thus restricting the occurrence of *G.* (*Geragnostella*) *fenhsiangensis* to the South China Plate.

G. (*Geragnostella*) *fenhsiangensis* is very similar to a number of species assigned to *G.* (*Geragnostella*) by Nielsen (1997). *G. occitanus* Howell, 1935 (see also Dean 1966: pl. 1, figs 1–12,

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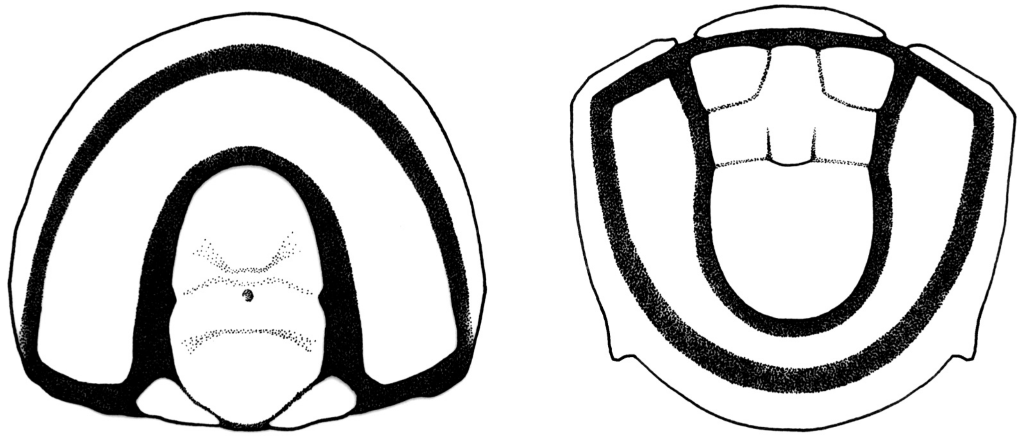

Figure 6 Reconstruction of the external exoskeletal surface of the cephalon and pygidium of *Geragnostus* (*Geragnostus*) *balanolobus* sp. nov., × 16.

pl. 2, figs 1, 7), from the Arenig of the Montagne Noire, has a similar subquadratic cephalon, with the glabella also appearing increasingly conical in flattened specimens, but has a shorter, more rounded pygidial posterolobe. *G. hispanicus* Rábano, Pek & Vaněk, 1985 (see also Rábano 1990: pl. 1, figs 1–7), from the lower Llanvirn of Spain, has a shorter pygidium, and *G. gilcidae* Rábano, Pek & Vaněk, 1985 (see also Rábano 1990: pl. 1, figs 8–14), also from the lower Llanvirn of Spain, has a pygidium which appears more rounded in both acrolobal and overall outline. *G. wimani* Tjernvik, 1956 (text-fig. 27D, pl. 1, figs 11–12; see also Ahlberg 1992, fig. 9a–q) has more parallel-sided cephalic and pygidial acrolobes and pygidial posterolobe, and deeper pygidial axial furrows. *G. lycaonicus* Dean, 1971 (pl. 1, figs 1, 3, 5, 7–8), from the Arenig of S Turkey, is known from very little material, but has a longer pygidial posterolobe and acrolobe.

Geragnostus tullbergi (Novák, 1883), the type species of *G.* (*Geragnostella*), was redescribed by Ahlberg 1989b (p. 557, pl. 61, figs 1–15, pl. 62, figs 1–3). This species has a more parallel-sided glabella, narrower border furrows, and a posterolobe, acrolobe and overall pygidial outline that are more laterally and posteriorly rounded. *Geragnostus semipolitus* Dean, 1973 (pl. 1, figs 2, 4–5, 7–12, 14), from the Arenig of S Turkey, is morphologically very similar to *G. tullbergi*, and was regarded as a junior synonym of that species by Ahlberg (1989b). An agnostid cephalon from Maocaopu (Fig. 7i) is parallel-sided in acrolobal and glabellar outline and is morphologically very similar to that of *G. tullbergi*, but is associated with pygidia identical to those of *G.* (*Geragnostella*) *fenhsiangensis* (Fig. 7o); as the cephalon is unflattened, unlike those from Daping, this variation is interpreted as taphonomic rather than taxonomically significant.

Geragnostus? *carinatus* Lu, 1975
Figure 7p

1975 *Geragnostus carinatus*; Lu, p. 91 (277), pl. 1, figs 5–7, *non* fig. 8 [=Metagnostidae gen. et sp. indet.].
1977 *Geragnostus carinatus* Lu; Zhou *et al*., p. 109, pl. 36, fig. 12, *non* fig. 13. [=Metagnostidae gen. et sp. indet.].
1987 *Geragnostus carinatus* Lu; Zhou, p. 657.
1997 *Geragnostus* (*Geragnostus*?) *carinatus* Lu; Nielsen, p. 483.
1999 *Geragnostus* (*Geragnostus*?) *carinatus* Lu; Nielsen, p. 62.

Holotype. Cephalon (NI 16366); figured Lu (1975: pl. 1, fig. 5).

Type stratum and type locality. Member 3, Dawan Formation, upper Arenig Series, Panguzhai, Tangya, Yichang County, W Hubei, China.

Material. One cephalon (NI 133821) from Bed 6 of the Dawan Formation at Daping.

Description. Cephalon subovoid; maximum width (tr.), at cephalic midline (sag.), approximately equal to maximum length (sag.). Posterior margin with tiny posterolateral spines. Glabella occupies 55 per cent cephalic length (sag.) and 60–65 per cent acrolobe length. Maximum glabellar width excluding basal lobes (tr.), opposite anterior margin of basal lobes and opposite F3, equal to 35 per cent maximum cephalic width (tr.); maximum glabellar width including basal lobes, at posterior margin of glabella, 40 per cent maximum cephalic width. Basal lobes very short (exsag.), barely meeting at posterior margin of cephalic midline (tr.). Axial furrows *en grande tenue*, approximately parallel for at least posterior 50 per cent of their length, disrupted by rather marked adaxial notch at F2; converging opposite the anterior 35 per cent of glabella to produce a rounded trapezoidal anterior glabellar margin. Faint median keel extends anteriorly for 35 per cent glabellar length from posterior glabellar margin. Glabellar furrows largely effaced; F3 faintly visible at 60–70 per cent distance from posterior glabellar margin; transverse medially, with anterior extensions laterally. Acrolobe subovoid. Flattened border extends anteriorly from position slightly anterior to posterior margin of acrolobe; anterior border 10 per cent cephalic length (sag.). Border furrow narrow and non-deliquiate. Parietal surface smooth.

Remarks. Lu (1975) established *Geragnostus carinatus* on the basis of three cephala with faint posteromedian keels, and a specimen (NI 16369; Fig. 7q; also figured Lu 1975: pl. 1, fig. 8; Zhou *et al*. 1977: pl. 36, fig. 13) which he interpreted as representing a pygidium with a short posterolobe. Both Lu (1975) and Nielsen (1997, 1999) commented on the unusual shortness of the pygidial axis compared to the condition displayed by other members of the genus; however, on the basis of pygidial characters, Nielsen (1997, 1999) considered that the species was best assigned to *G.* (*Geragnostus*). Re-examination of this 'pygidium' shows that in fact it represents a metagnostid cephalon with fairly generalised morphology, with a somewhat strongly defined median glabellar node. It lacks the median keel which characterises both the three cephala referred by Lu (1975) to *G. carinatus* and the new cephalon figured herein, and has a more prominent glabellar node than shown by any of these cephala, so is not considered conspecific. Due to the difficulty in assigning taxa to either *Geragnostus* or *Trinodus* on the basis of cephalic characters alone (see above), the taxonomic placement of NI 16369 can only be resolved to Metagnostidae gen. et sp. indet. Generic assignment of the various cephala representing *G. carinatus* is also unclear in the absence of a pygidium; they are tentatively

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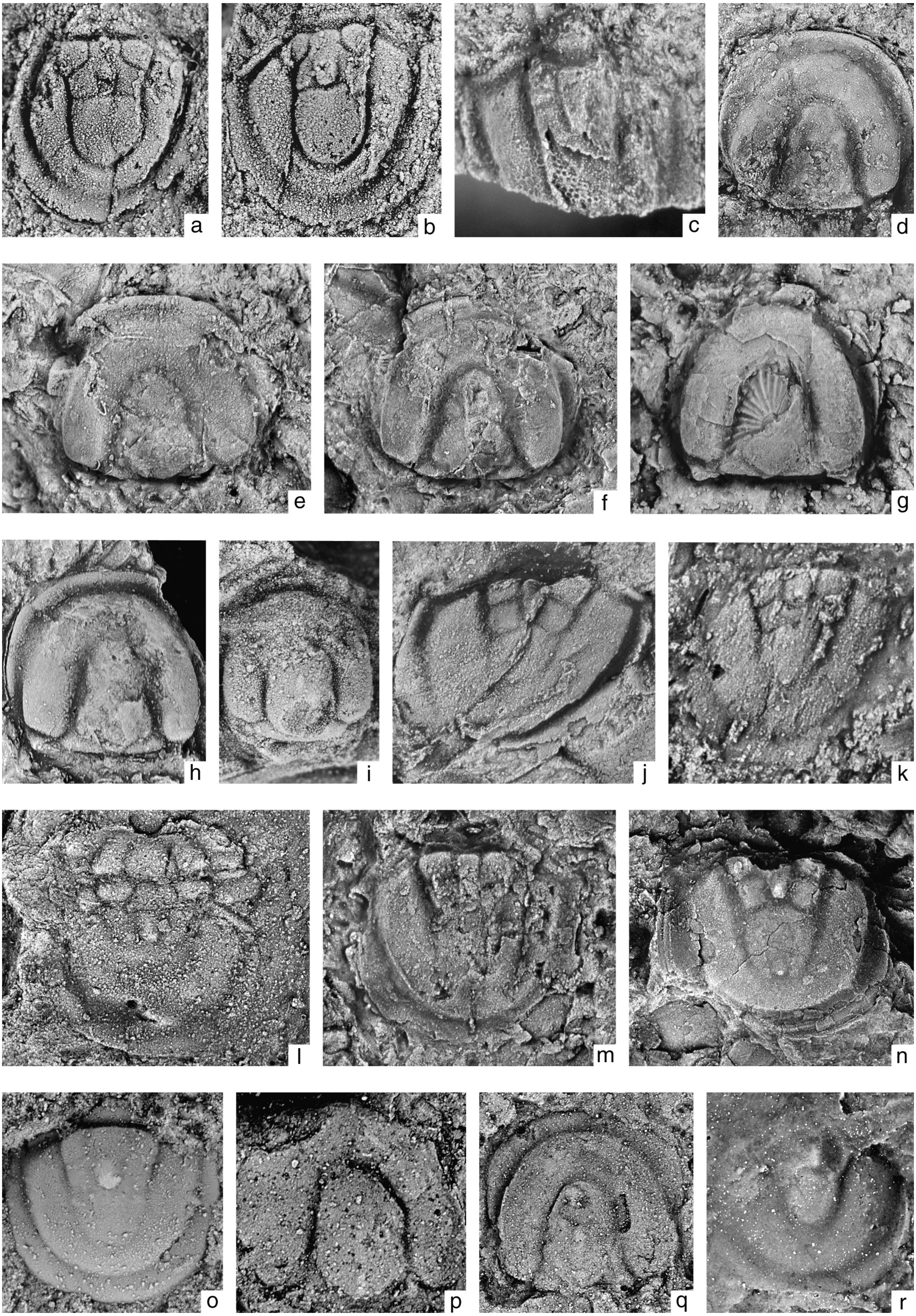

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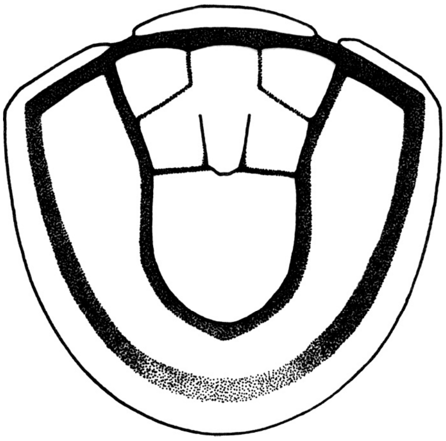

Figure 8 Reconstruction of the external exoskeletal surface of the pygidium of *Geragnostus* (*Geragnostus*) *waldorfstatleri* sp. nov., × 16. Cephalon as for *G.* (*G.*) *balanolobus*.

retained within *Geragnostus* until further material becomes available.

Geragnostus? subgen. et sp. indet.
Figure 7r

Material. One incomplete pygidium (NI 1338230) from Bed 4 of the Dawan Formation at Daping.

Remarks. A pygidial external mould from Daping, although incomplete, shows a distinctive narrow pygidial posterolobe with prominent axial furrows. It cannot be assigned to either *Trinodus hupehensis* or *Geragnostus* (*Geragnostus*) *balanolobus*, the two agnostid species recorded from this horizon and locality which have non-effaced pygidial axial furrows, as the posterolobe is longer and narrower than in *T. hupehensis*, and shorter and less swollen in outline than in *G.* (*G.*) *balanolobus*. The specimen is too incomplete to be used to establish a new species, and in the absence of an associated cephalon its generic placement is uncertain. If it represents a metagnostid, it should probably be assigned to *Geragnostus*, as its posterolobe morphology is closer to the condition displayed by this genus than to that of *Trinodus*.

3. Palaeoecology and biogeography of South Chinese agnostids

Agnostids are restricted to outer shelf and slope margin assemblages on the South China Plate during the Arenig–Llanvirn; this 'oceanic' occurrence in exterior facies is typical for the group (Palmer 1984; Zhou 1987; Fortey & Owens 1999; Peng & Robison 2000). *Geragnostus* and *Trinodus* are abundant in the diverse Asaphid–Raphiophorid and Trinucleid associations occurring in shallow outer shelf clastic facies from Member 3 of the Dawan Formation in W Hubei, and *Geragnostus* also ranges into the slightly shallower carbonate facies of Member 1 characterised by the Asaphid-*Pseudocalymene* Association (Turvey & Zhou 2002). These two genera remain abundant in coeval deeper carbonate and clastic facies in N Hunan represented by the Zitai and Jiuxi formations, occurring in both the Nileid–Illaenid and *Pseudopetigurus* associations, with rare material assigned to *Micragnostus*? and *Han* also found in the Zitai Formation (Turvey & Zhou 2004a). This palaeobathymetric distribution matches Nielsen's (1997) observation that, although Ordovician agnostids were generally more diverse in cold to temperate water regions, *Geragnostus* and *Trinodus* enter the interior of palaeoequatorial continents rather than being restricted to cratonic fringes, with the *elspethi* group of *Trinodus* characteristic of warmer water and rare or absent at high palaeolatitudes; Cambrian–earliest Ordovician representatives of the Agnostidae and Pseudagnostinae instead occur in deeper water low-oxygen facies. Fortey (1975) also interpreted *Micragnostus* as typical of the deep water Olenid Association.

Agnostids have never been recorded from the shallow inner shelf region of the South China Plate, despite extensive research conducted into the Arenig and Llanvirn trilobite faunas from S Shaanxi over the past century (e.g. Pellizzari 1913; Endo 1932; Kobayashi 1951; Li *et al*. 1975; Lu 1975; Zhou *et al*. 1982; Chen & Zhou 2002; Turvey & Zhou 2004b). Although numerous representatives of the diverse Arenig–Llanvirn benthic trilobite faunas of the Yangtze Platform also occur on the proximal Tarim Plate and Indo-China Terrane (Zhou *et al*. 1998a, b; Turvey & Zhou 2004b), leading to these three units being considered as a single biogeographic region by Turvey (2005a), agnostids are also absent from the latter regions during this interval (Zhou *et al*. 1992; Zhou Zhiyi pers. comm. 2004). All of the agnostid species described herein appear to be biogeographically restricted to the South China Plate, and increasing agnostid cosmopolitanism only occurs during the global breakdown of benthic trilobite endemicity in the Late Ordovician (Cocks 2001).

Agnostid autecology remains a disputed and poorly understood area of trilobite palaeoecology; pelagic, benthic, and more specialised alternate modes of life have been advocated by various authors on the basis of various lines of evidence including comparative morphology, biofacies analysis and taphonomy (see reviews in Fortey & Owens 1999 and Turvey & Zhou 2004a). The facies dependence and range restriction displayed by South Chinese agnostids contrast with the wide geographic distributions shown by uncontroversially pelagic Ordovician arthropods, which are constrained by palaeolatitude rather than facies or plate boundaries (Fortey 1985; Rigby & Milsom 2000; Vannier *et al*. 2003). The epipelagic *Carolinites genacinaca* Ross, 1951 displays the most cosmopolitan distribution of any trilobite (McCormick & Fortey 1999) and occurs across inner and outer shelf facies on the Yangtze Platform and Jiangnan Transitional Belt during the Arenig (Turvey & Zhou 2002, 2004a, b), and other deeper-water pelagic trilobites recorded from South China (see Turvey & Zhou 2004a, b) are typically also known from coeval strata on non-contiguous palaeoplates (e.g. Marek 1961; Henderson 1983).

Figure 7 (a–c) *Geragnostus* (*Geragnostus*) *waldorfstatleri* sp. nov.: Bed 3, Panjiazui; (a) pygidium, NI 133809, × 15; (b) pygidium (holotype), NI 133804, × 15; (c) pygidium, NI 133810, × 12. (d–o) *Geragnostus* (*Geragnostella*) *fenhsiangensis* Lu, 1975: (d) cephalon, NI 134043, × 6, Bed 6, Daping; (e) cephalon, NI 133813, × 8, Bed 6, Daping; (f) cephalon, NI 133814, × 7, Bed 7, Daping; (g) cephalon, NI 133815, × 6, Bed 7, Daping; (h) cephalon, NI 133812, × 8, Bed 6, Daping; (i) cephalon, NI 133870, × 15, Bed 2, Maocaopu; (j) pygidium, NI 133811, × 9, Bed 3, Panjiazui; (k) pygidium, NI 134084, × 15, Bed 3, Panjiazui; (l) thoracopygon, NI 133820, × 15, Bed 1, Shuanghong; (m) pygidium, NI 133818, × 12, Bed 5, Daping; (n) pygidium, NI 133816, × 8, Bed 6, Daping; (o) silicone rubber cast of pygidium, NI 133817, × 15, Bed 2, Maocaopu. (p) *Geragnostus*? *carinatus* Lu, 1975: cephalon, NI 133821, × 15, Bed 6, Daping. (q) Metagnostidae gen. et sp. indet.: cephalon, NI 16369, × 10, Member 3, Dawan Formation, Panguzhai, Tangya, Yichang County, W Hubei (figured Lu 1975: pl. 1, fig. 8 and Zhou *et al*. 1977: pl. 36, fig. 13 as *Geragnostus carinatus*). (r) *Geragnostus*? subgen. et sp. indet.: silicone rubber cast of pygidium, NI 133823, × 15, Bed 4, Daping.

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These differences indicate that South Chinese agnostids were probably benthic or epibenthic rather than pelagic. This interpretation is supported by the relatively large body size of some South Chinese agnostids, notably *G.* (*Geragnostella*) *fenhsiangensis* (cephala and pygidia up to 6 mm in length). Indeed, the range of families represented by the South Chinese outer shelf agnostids suggests that a benthic mode of life may represent the primary ecology of the order. The facies dependence and distribution of some non-Gondwanan agnostids is also similar to that shown by benthic macrofaunal fossils during the Ordovician (Ahlberg 1992). However, the restricted ranges of Ordovician agnostids differ markedly from the geographic cosmopolitanism displayed by many Cambrian agnostid species, which in conjunction with their typically rapid evolution and concomitant narrow stratigraphic ranges has led to their extensive use in global biozonation (e.g. Peng & Robison 2000). Arenig–Llanvirn species of both *Trinodus* and *Geragnostus* occur in Baltica and Laurentia as well as Gondwanan and peri-Gondwanan regions, and both taxa have been used as 'wastebasket' genera by many authors (around 100 species have variously been assigned to *Geragnostus*), and so may contain numerous synonyms (Nielsen 1997, 1999). Biogeographic patterns shown by Ordovician metagnostids thus remain difficult to determine, and it is possible that some species may have been considerably more cosmopolitan than is currently recognised.

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