

REVIEW OF EARLY TRIASSIC THYLACOCEPHALA

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Abstract. Thylacocephala (Euarthropoda: Eucrustacea?) is a group of enigmatic fossil euarthropods, known from at least the Silurian to the Cretaceous. The Triassic is considered to be the period during which thylacocephalans were the most diversified with 17 species reported from 19 localities in nine countries. However, Thylacocephala were assumed to be rare during the Early Triassic until recent discoveries in Japan, Nevada and Idaho, U.S.A.

Our study focuses on thylacocephalans from the Early Triassic, especially from Madagascar and Idaho. The revision of previously known taxa from Madagascar provides new important information. A new kind of ornamentation is reported for *Paraostenia ambatolokobensis* nov. comb., previously assigned to *Ostenocaris ambatolokobensis*. In addition, *Ankitokazocaris acutirostris* and *Paraostenia ambatolokobensis* are only the third and fourth thylacocephalan taxa for which possible cephalic appendages are described.

New occurrences of Thylacocephala in Nevada and Idaho, U.S.A., lead to the description of one new taxon and to the reassignment of *Parisicaris triassica* to *Ankitokazocaris triassica* nov. comb. Those occurrences provide a significant contribution to the knowledge of Thylacocephala taxonomic diversity and geographic distribution during the Early Triassic. An important revision of Early Triassic thylacocephalan taxa from Japan and China is also performed, including *Ankitokazocaris chaobuensis*, *Ankitokazocaris parva* nov. comb., *Ankitokazocaris utatsuensis* nov. comb. and *Paraostenia* sp. Overall, the taxonomic diversity of Triassic thylacocephalans has likely been slightly over-estimated (17 species before, 15 now). However, the Triassic represents the richest period in terms of thylacocephalan-bearing outcrops (19 localities from nine countries).

INTRODUCTION

Thylacocephala Pinna, Arduini, Pesarini & Teruzzi, 1982 is an enigmatic fossil euarthropod in-group identified by particular body traits: a prominent sclerotized shield [*carapace*] enveloping almost

the entire body, large compound eyes, three pairs of large raptorial appendages protruding from under the shield, often eight sets of gills and from eight up to twenty-two posterior trunk segments bearing appendages. Despite this knowledge on their anatomy, the phylogenetic affinities of Thylacocephala remain unclear, some morphological details supporting a position within Eucrustacea (Broda & Zatoń 2017; Haug et al. 2014; Vannier et al. 2016). The

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Age		Distribution	Taxa	References
Early Triassic	Dienerian-Smithian	Madagascar	<i>Ankitokazocaris acutirostris</i> Arduini, 1990	Arduini 1990; this paper
			<i>Paraostenia ambatolokobensis</i> (Arduini, 1990) nov. comb.	Arduini 1990; this paper
	Smithian	Australia	Austriocarididae	Haig et al. 2015
	early Spathian	U.S.A.	<i>Ankitokazocaris triassica</i> (Charbonnier in Charbonnier et al., 2019) nov. comb.	Charbonnier et al. 2019; this paper
			<i>Ligulacaris parisiana</i> Charbonnier in Charbonnier et al., 2019	Charbonnier et al. 2019 ; this paper
			Thylacocephala indet.	This paper
	Spathian	Japan	<i>Ankitokazocaris bandoi</i> Ehiro et Kato in Ehiro et al., 2015	Ehiro et al. 2015
			<i>Ankitokazocaris chaohuensis</i> Ji, Tintori, Jiang & Motani, 2017	Ehiro et al. 2015; this paper
			<i>Ankitokazocaris parva</i> (Ehiro, Sasaki, Kano & Nagase, 2019) nov. comb.	Ehiro et al. 2019; this paper
			<i>Ankitokazocaris utatsuensis</i> (Ehiro et Kato in Ehiro et al. 2015) nov. comb.	Ehiro et al. 2015; this paper
			<i>Paraostenia</i> sp.	Ehiro et al. 2015; this paper
			<i>Ostenocaris?</i> sp.	Ehiro et al. 2019
	late Spathian	China	<i>Ankitokazocaris chaohuensis</i> Ji, Tintori, Jiang & Motani, 2017	Ji et al. 2017; this paper
Middle Triassic	Anisian	China	? <i>Atropicaris</i> sp.	Feldmann et al. 2015
			<i>Yangzicaris xiangxiensis</i> Yan-bin, 1983	Yan-bin 1983
		Italy	<i>Microcaris</i> sp.	Teruzzi & Muscio 2019
			<i>Microcaris minuta</i> Pinna, 1974	Pinna 1974
			Thylacocephala indet.	Teruzzi & Muscio 2019
	Ladinian	Slovenia	<i>Microcaris minuta</i> Pinna, 1974	Križnar & Hitij 2010
		Spain	<i>Ferreccaris magransi</i> Calzada & Mañé, 1993	Calzada & Mañé 1993
Late Triassic	Carnian	Austria	<i>Austriocaris carinata</i> Glaessner, 1931	Forchielli & Pervesler 2013; Glaessner 1931
			<i>Atropicaris striata</i> (Glaessner, 1931)	Glaessner 1931
	Norian	Italy	<i>Clausocaris pinnai</i> Arduini, 1992	Arduini 1992
			<i>Microcaris minuta</i> Pinna, 1974	Arduini 1988; Dalla Vecchia 1993; Dalla Vecchia & Muscio 1990; Pinna, 1976
	Rhaetian	Italy	<i>Microcaris rostrata</i> (Arduini & Brasca, 1984)	Arduini 1988; Arduini & Brasca 1984; Teruzzi & Muscio 2019; Tintori et al. 1986

Tab. 1 - List of Triassic Thylacocephala.

palaeoecology of Thylacocephala is also problematic. Various lifestyles including predatorial (Secrétan 1985; Vannier et al. 2016), necrophageous (Pinna et al. 1985) or filter-feeding (Pinna et al. 1982) have been proposed and the question is still debated.

Thylacocephalans have a global palaeogeographic distribution, known from all continents except Antarctica and South America (Hegna et al. 2014). They also have a wide stratigraphic range, being known from at least the Silurian (Haug et al. 2014), and possibly from the Ordovician (*Decoracaris hildebrandi* Briggs, Liu, McKay & Witzke, 2015 from the Winneshiek Lagerstätte, Iowa, U.S.A.), to the Cretaceous (several species from Lebanon: Charbonnier et al. 2017; Lange et al. 2001; Schram et al. 1999).

During the Triassic, thylacocephalans were diversified and widely distributed within low-latitude regions (Ehiro et al. 2019). The Triassic was thus considered to be the period during which representatives of Thylacocephala were the most diversified (Charbonnier et al. 2019). Seventeen species have been reported from 19 localities in nine countries (Tab. 1; Australia: Haig et al. 2015; Austria: Forchielli & Pervesler 2013; Glaessner 1931; China: Feldmann et al. 2015; Ji et al. 2017; Yan-bin 1983; Italy: Affer & Teruzzi, 1999; Arduini 1988, 1992; Arduini & Brasca 1984; Dalla Vecchia 1993; Dalla Vecchia & Muscio 1990; Pinna 1974, 1976; Teruzzi & Muscio 2019; Japan: Ehiro et al. 2015, 2019; Madagascar: Arduini 1990; U.S.A.: Charbonnier et al. 2019; Slovenia: Križnar & Hitij 2010; Spain: Calzada & Mañé 1993).

We focus our study on representatives of Thylacocephala from the Early Triassic, especially from Madagascar and from the Paris Biota (Idaho, U.S.A.). In the Early Triassic, thylacocephalans were considered to be rare until recent discoveries (Charbonnier et al. 2019; Ehiro et al. 2015, 2019; Ji et al. 2017). Among the 17 Triassic species, nine were described from Lower Triassic localities (China, Japan, Madagascar, U.S.A.; Tab. 1). The revision of previously known taxa from Madagascar provides new important information on the micro-ornamentation and on cephalic appendages of Thylacocephala. In addition, this descriptive work led to an extensive revision of Early Triassic taxa from Japan and China.

GEOLOGICAL SETTINGS

Ankitokazo basin, northwestern Madagascar

During the Early Triassic, northwestern Madagascar was located in Gondwana (palaeolatitude of ca. 40°S and palaeolongitude of ca. 60°E; Ricou 1994) and Ankitokazo basin (Diégo-Suarez Province, northwestern Madagascar; Fig. 1) witnessed deposition in a neritic environment. Due to the transgression of the Tethys sea, a channel invaded the Ankitokazo basin, forming an epicontinental warm and shallow sea, with an average depth of 200–300 m (Besairie 1972).

The marine Lower Triassic localities from the Ankitokazo basin yield a rich and well-diversified non-vertebrate fauna (Ammonoidea: Besairie 1972; Collignon 1934; Annelida: Alessandrello 1990; Bivalvia: Besairie 1972; Eucrusteracea: Brambilla et al. 2002; Charbonnier et al. 2012; Garassino et al. 2003; Garassino & Pasini 2002; Garassino & Teruzzi 1993; Van Straelen 1933; Yan-bin et al. 2002; Xiphosura: Hauschke et al. 2004) and a vertebrate fauna (Actinopterygii & Sarcopterygii: Beltan et al. 1996; Marramà et al. 2017; Piveteau 1934; Lissamphibia: Rage & Roček 1989; Steyer 2002; Reptilia: Falconnet et al. 2012; Ketchum & Barrett 2004) but only few terrestrial plant remains (Hankel 1993). Among these taxa, two species of Thylacocephala were described: *Ankitokazocaris acutirostris* Arduini, 1990 and *Ostenocaris ambatolokobensis* Arduini, 1990.

The marine Lower Triassic fauna was described by Besairie (1972) as a single assemblage from the Middle Sakamena Formation. This formation is composed of various members highly variable

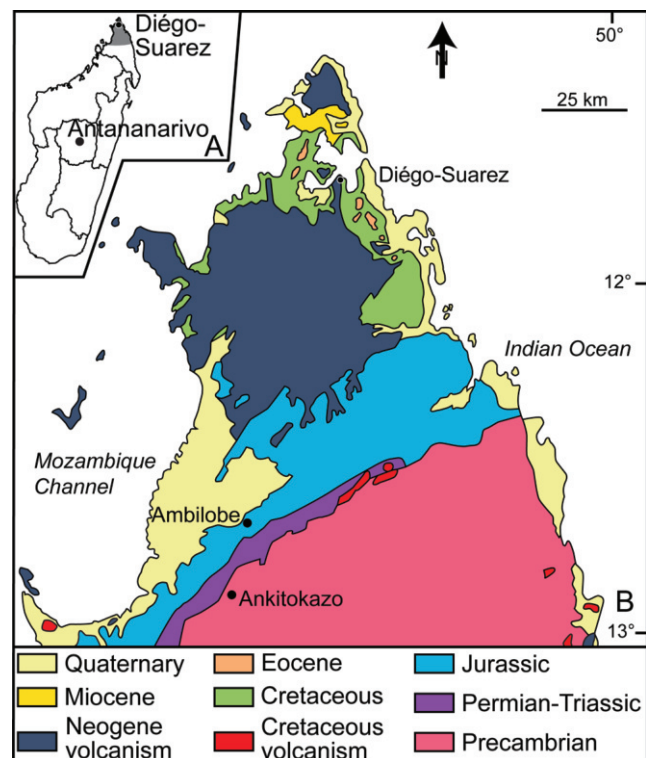


Fig. 1 - Geology of northwestern Madagascar. A: Location of the area of interest in Madagascar (grey zone). B: Simplified geological map of northwestern Madagascar (after Besairie 1964).

in thickness (300–600 m). However, no indications are currently available on its stratigraphy including the exact position of the fossiliferous horizon (Marramà et al. 2017). The Middle Sakamena Formation is divided into two parts: the fossiliferous lower part (“Couches à Poissons et Ammonites”), made of clayey shales with continental sandstone intercalations, and the non-fossiliferous upper part (“Schiste d’Ira-ro”), formed of shales. The age of the Sakamena Formation is still discussed: Beltan (1996) and Steyer (2002) documented actinopterygians, sarcopterygians and amphibians as being from the Dienerian (late Induan), while Yan-bin et al. (2002) determined a Smithian age (early Olenekian) based on conchost-racans. Following Marramà et al. (2017), we consider our specimens to be Dienerian/Smithian in age.

In the Middle Sakamena Formation, fossils are generally preserved in siliceous nodules found in laminated marly limestones/mudstones. They are formed of 77.9% of silica, 11.1% of iron oxides, 5.2% of clay and titanium oxide and 5.7% of other trace minerals (Besairie 1972). However, their full diagenetic history has never been studied thoroughly.

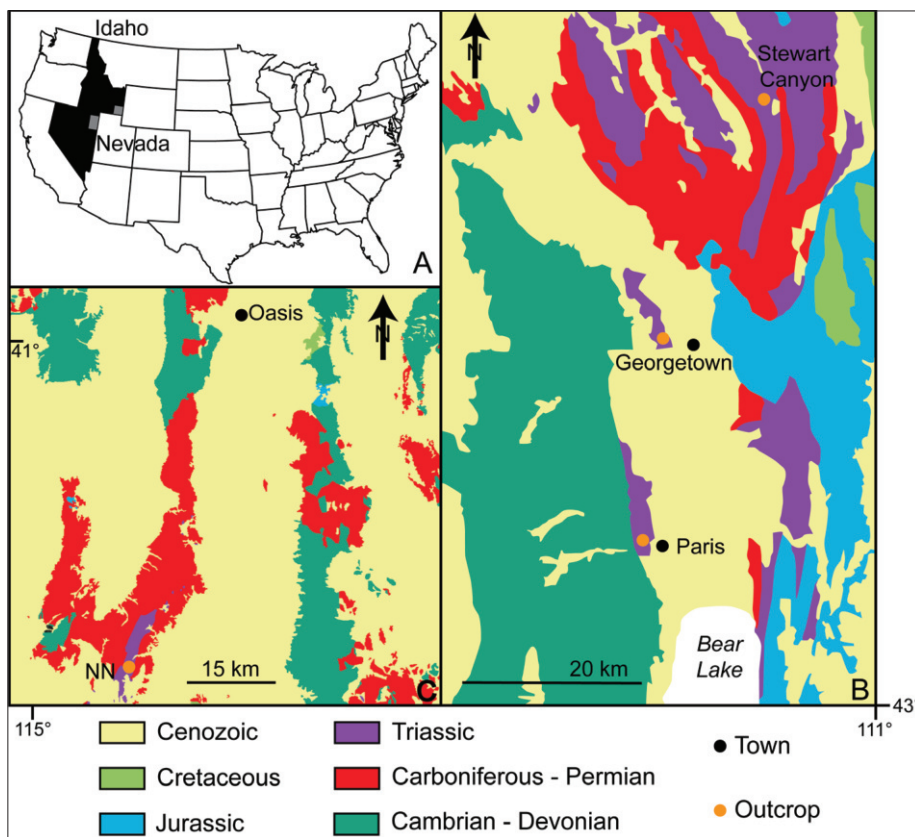


Fig. 2 - Geology of Eastern U.S.A. A: Location of areas of interest in U.S.A (grey zone). B, C: Simplified geological map of southeastern Idaho (after Oriol et al. 1980) and northeastern Nevada, showing location of sampled fossiliferous sites.

U.S.A.

The Paris Biota (early Spathian, Early Triassic, Bear Lake County, southeastern Idaho, U.S.A; Fig. 2) documents a remarkably well-diversified multi-levelled marine ecosystem, with the presence of primary producers up to top predators and potential scavengers (Brayard et al. 2017). It yielded Porifera (Botting et al. 2019), Brachiopoda, Bivalvia, Nautiloidea (Brayard et al. 2019b), Ammonoidea, gladius-bearing Coleoidea (Doguzhaeva et al. 2018), belemnoid hooks, Euarthropoda (Charbonnier et al. 2019), Ophiuroidea (Thuy et al. 2019), Crinoidea (Saucède et al. 2019), Vertebrata (Romano et al. 2019), and algae. The Paris Biota shows a functionally complex marine ecosystem only ~2.6 My after the end-Permian mass extinction (Widmann et al. 2020), of which the exact spatiotemporal distribution has yet to be determined (Brayard et al. 2017). Long-ranging Palaeozoic taxa are associated with derived clades who originated at least in the pre-Spathian. Among Euarthropoda, two species of Thylacocephala have been described: *Parisicaris triassica* Charbonnier in Charbonnier et al., 2019 and *Ligulacaris parisiana* Charbonnier in Charbonnier et al., 2019.

The Paris Biota belongs to the lower Spathian Lower Shale Unit of the Lower Triassic Thaynes Group. Marine sediments of the Thaynes Group were deposited in the western U.S.A. basin, presently mostly covering Utah, eastern Nevada, eastern Idaho and western Wyoming. During the Early Triassic, this basin was bordered by the Permian-Triassic Sonoma orogeny to the West (Blakey & Ranney 2018). This basin was located at an almost palaeo-equatorial position on the western margin of Pangaea and mainly consisted of a relatively shallow epicontinental environment (e.g., Caravaca et al. 2018). This group consists of an alternation of limestones and shales (Lucas et al. 2007). Most fossils of the Paris Biota are compressed, but preserve some three-dimensional features. Porifera, Euarthropoda, Brachiopoda, and vertebrate coprolites are preserved in calcium phosphate suggesting rapid decay and burial in phosphatizing microenvironments (Iniesto et al. 2019). Two newly discovered sites (Stewart Canyon and Georgetown; Fig. 2) from the same area and very same age as the Paris Biota and a new site from eastern Nevada, U.S.A. also from the same age (C. P. A. Smith and A. Brayard, ongoing work) provided specimens of Thylacocephala.

During the Early Triassic, several episodic environmental and climatic events affected the biodiversity (Grasby et al. 2013; Payne et al. 2004; Romano et al. 2013). One of them corresponds to the Smithian-Spathian boundary (e.g., Galfetti et al. 2007; Zhang et al. 2019), which recorded a severe loss of biodiversity, especially within the nektonic groups (e.g., Tozer 1982; Brayard et al. 2006; Orchard 2007). This selective extinction coincided with a major global climate change. The late Smithian was subject to renewed, large-scale perturbations of the global biogeochemical cycles including a large $\delta^{15}\text{C}$ positive excursions and a marked cooling (Goudemand et al. 2019; Widmann et al. 2020). Following the late Smithian extinction event, the early Spathian represents a time of rapid diversification, as exemplified by the diversified and multi-levelled marine ecosystem of the Paris Biota.

MATERIAL & METHODS

Material

Madagascar. The present study is based on 33 thylacocephalan specimens housed in the collections of the Museo Civico di Storia Naturale di Milano, Italy (MSNM) and of the Muséum national d'Histoire naturelle, Paris, France (MNHN). It includes holotypes and paratypes of *Ankitokazocaris acutirostris* and *Paraostenia ambatolokobensis* nov. comb.

U.S.A. 15 specimens, including the holotypes and paratypes of *Ankitokazocaris triassica* nov. comb. and *Ligulacaris parisiana* were studied. They are housed in the palaeontological collections of the Université de Bourgogne, Dijon, France (UBGD) and of the Idaho Museum of Natural History, Pocatello, Idaho, U.S.A (IMNH). Additional material was collected during scientific missions in 2018 and 2019 by the Paris Biota team.

Documentation methods & image processing

Madagascar. Specimens from the MSNM were documented with a NIKON D700 camera and a NIKON AF-S NIKKOR 35mm f/1.8g ED lens. Counter part of MNHN.FA72327 was documented using a NIKON D5300 camera and a NIKON AF-S NIKKOR 35mm f/1.8g ED lens equipped with a HOYA HD polarising filter and illuminated with a Kaiser RB 218n HF lighting unit. MNHN.FA72326 and part of MNHN.FA72327 were documented with a Canon Rebel T3i camera and a Canon MPE-65 mm macro lens equipped with a HOYA HD polarising filter and illuminated with a Kaiser RB 218n HF lighting unit. To overcome limitations in depth of field and in field of view, several adjacent image details were recorded for the part, each with a Z-stack of images.

Z-stacks of images were digitally fused to single in-focus images using CombineZP (Alan Hadley, GPL). These fused images were stitched together with Image Composite Editor. Post-processing of every image (histogram optimisation, contrast and brightness adjustment) was performed with Adobe Photoshop CS5. Additionally, areas of interest were colour-marked to highlight morphological structures. Line drawings were prepared using Adobe Illustrator CS6.

U.S.A. As thylacocephalans from the Paris Biota and the new Georgetown and Stewart Canyon sites are distinctly autofluorescent under various settings (Brayard et al. 2019a), we acquired images under different illumination/detection couples at the IPANEMA laboratory (Gif-sur-Yvette, France). To do so, we used different transmission interferential filters positioned in front of a Si EM-CCD coupled to an apochromatic 60 mm lens. The specimens were illuminated under different selected wavelengths ranging from UV to NIR thanks to LED lights. For each specimen, fluorescent images were used to produce a single composite image using ImageJ2 (GPL, Schneider et al. 2012). Post-processing of every composite image (histogram optimisation, contrast and brightness adjustment) was performed with ImageJ2.

IMNH 288/1701 was documented using a NIKON D5300 camera and a NIKON AF-S NIKKOR 35mm f/1.8g ED lens and illuminated with a Kaiser RB 218n HF lighting unit. The images were then processed with Adobe Photoshop CS5 (histogram optimisation, contrast and brightness adjustment). Line drawings were made using Adobe Illustrator CS6.

Measurements

Measurements (Fig. 3) were taken directly from digital photographs with ImageJ2. When part and counter-part were available, measurements were done on both sides and then averaged. The list of measurements and the R script for descriptive statistics are available on Zenodo repository:

<https://doi.org/10.5281/zenodo.4066340>

The following dimensions have been measured: A_{ad} = antero-dorsal angle, A_{av} = antero-ventral angle, A_{pd} = postero-dorsal angle, A_{pv} = postero-ventral angle, d = diameter, ha = anterior shield height, h_{max} = maximal shield height, h_p = posterior shield height, l = length, l_r = length of the rostrum, l_s = length of the shield, l_w = length without rostrum, w = width.

Institutional abbreviations

IGPS: Institute of Geology and Paleontology, Tohoku University Museum, Japan.

IMNH: Idaho Museum of Natural History, Pocatello, Idaho, U.S.A.

MNHN: Muséum national d'Histoire naturelle, Paris, France.

MSNM: Museo Civico di Storia Naturale di Milano, Italy.

NIGP: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

UBGD: Université de Bourgogne, Dijon, France.

UIM: Utatsu Ichthyosaur Museum, Miyagi Prefecture, Japan.

SYSTEMATIC PALAEOLOGY

Preliminary remarks. Schram (2014: 359) made an attempt to classify Thylacocephala. However, as mentioned by the author, “the scheme of classification proposed here [in Schram 2014] for Thylacocephala is not perfect”. His classification is based on a phylogenetic analysis made manually using the method of Hennig on a restricted number of taxa. The matrix is not provided which is a main problem to test its reproducibility and thus this classification. Moreover, some of the groups defined by Schram (2014) are not defined by proper

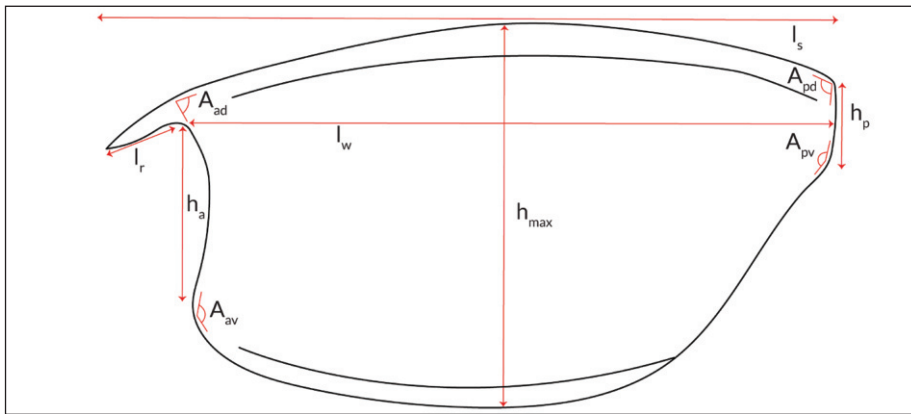


Fig. 3 - Scheme of measurements. Abbreviations: A_{ad} , antero-dorsal angle; A_{av} , antero-ventral angle; A_{pd} , postero-dorsal angle; A_{pv} , postero-ventral angle; h_a , anterior shield height; h_{max} , maximum shield height; h_p , posterior shield height; l_r , length of the rostrum; l_s , length of the shield; l_w , length without rostrum.

autapomorphies and may not represent monophyletic groups. For instance, Schram defined Conchyliocarida and Concavicularida, the two most inclusive taxa. The autapomorphies of Conchyliocarida are: an extreme hypertrophy of compound eyes, subchelate claws robustly formed, armored and spinose and generally 16 posterior trunk somites bearing paddle-like appendages. All taxa included in Conchyliocarida, with the exception of *Thylacares brandonensis* C. Haug, Briggs, Mikulic, Kluessendorf & J. T. Haug, 2014, have between 8 to 10 posterior trunk segments [Arduini et al. 1980 for *Ostenocaris*; Vannier et al. 2016 for *Dollocaris ingens* (Van Straelen, 1923)]. Moreover, the trunk appendages are not paddle-like, but are styliform for *Dollocaris ingens* (Secrétan, 1985) and *Mayrocaris bucculata* Polz, 1994.

For Concavicularida, Schram (2014) defined the following autapomorphies: a rostrum (developed in a variety of ways), optic notches as either moderate in size, or in some families rather undefined antero-ventrally, only 8 posterior trunk somites with weakly developed paddle-like limbs and raptorial chelae that appear as rather gracile in form. First, the definition is ambiguous. For instance, the presence of a rostrum is defined as an autapomorphy of this group but *Clausocaris* (Openheim, 1888) and *Convexicaris* Schram, 1990 do not have a rostrum, while *Dollocaris* Van Straelen, 1923 and *Kilianicaris* Van Straelen, 1923, usually attributed to Conchyliocarida, have a rostrum. Moreover, at least 14 trunk somites has been described in *Ankitokazocaris chaobuensis* Ji, Tintori, Jiang & Motani, 2017 and eleven in *Clausocaris lithographica* (Haug et al. 2014), which is in contradiction with the definition of Schram (2014) for Concavicularida. Based on these observations and following Hegna et al. (2014), we decided not to follow this classification.

Thylacocephala Pinna, Arduini, Pesarini & Teruzzi, 1982

Ankitokazocaris Arduini, 1990

Fig. 4

- 1990 *Ankitokazocaris* Arduini, p.199
- 2006 *Ankitokazocaris* – Vannier et al., fig. 3.9, tab. 1
- 2014 *Ankitokazocaris* – Hegna et al., p. 609
- 2014 *Ankitokazocaris* – Schram, p. 350
- 2015 *Ankitokazocaris* – Broda et al., fig. 4.9, tab. 1
- 2015 *Ankitokazocaris* – Ehiro et al., p. 272.
- 2015 *Kitakamicaris* Ehiro & Kato in Ehiro, Sasaki, Kano, Nemoto & Kato, p.274. nov. syn.
- 2017 *Kitakamicaris* – Charbonnier et al., p.14
- 2017 *Ankitokazocaris* – Ji et al., p.174
- 2019 *Parisicaris* Charbonnier in Charbonnier, Brayard & The Paris Biota team, p.38. nov. syn.
- 2019 *Kitakamicaris* – Charbonnier et al., p.38
- 2019 *Ankitokazocaris* – Ehiro et al., p.324, tab. 1
- 2019 *Kitakamicaris* – Ehiro et al., p.328
- 2019 *Miyajicaris* Ehiro, Sasaki, Kano & Nagase, p.324. nov. syn.
- 2019 *Ankitokazocaris* – Teruzzi & Muscio, p. 54
- 2019 *Parisicaris* – Teruzzi & Muscio, p. 54
- 2019 *Kitakamicaris* – Teruzzi & Muscio, p. 54
- 2020 *Ankitokazocaris* – Broda et al., p.16

Type species. *Ankitokazocaris*: *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar) by monotypy.

Included species. *Ankitokazocaris bandoi* Ehiro & Kato in Ehiro et al., 2015; Spathian, late Olenekian, Early Triassic, Japan – *Ankitokazocaris chaobuensis* Ji, Tintori, Jiang & Motani, 2017; Spathian, late Olenekian, Early Triassic, China & Japan – *Ankitokazocaris parva* (Ehiro, Sasaki, Kano & Nagase, 2019) nov. comb.; Spathian, late Olenekian, Early Triassic, Japan – *Ankitokazocaris triassica* (Charbonnier in Charbonnier et al., 2019) nov. comb.; early Spathian, late Olenekian, Early Triassic, U.S.A. – *Ankitokazocaris utatsuensis* (Ehiro & Kato in Ehiro et al., 2015) nov. comb.; Spathian, late Olenekian, Early Triassic, Japan.

Emended diagnosis. Thylacocephala with a folded shield; dorsal midline gently convex; anterior, triangular-shaped rostrum curved antero-ventrally; well-developed, asymmetrical optic notch; ventral margin subdivided into a sub-horizontal anterior part and a posterior part steeply descending antero-ventrally; posterior margin short, sub-vertical.

Remarks. *Ankitokazocaris* was a widespread taxon during the Early Triassic. With the reinterpretation of *Parisicaris* as *Ankitokazocaris*, it is now known from all Lower Triassic outcrops bearing representatives of Thylacocephala (Fig. 4), with the exception of Western Australia (Haig et al. 2015).

Charbonnier et al. (2019: figs 2a–c, 3) erected *Parisicaris* with *Parisicaris triassica* as the type species. New observations proved that the diagnostic ventral notch was an artefact of preparation. The present review of the holotype and the description of newly discovered specimens proved that they have a morphology diagnostic of *Ankitokazocaris*: a sharp, triangular-shaped rostrum, a gently convex dorsal midline, a short posterior margin, an anterior margin divided in a dorsal, well-developed optic notch and a convex ventral part (Fig. 4F). Thus, we consider *Parisicaris* as a junior synonym of *Ankitokazocaris*.

Two thylacocephalan taxa from Japan also fit in *Ankitokazocaris*: *Kitakamicaris* and *Miyagicaris*. They were two monospecific genera described from the upper Olenekian Osawa Formation in Japan (Ehiro et al. 2015, 2019). Their morphologies are similar: they differ only by their size. *Miyagicaris* was described based on two incomplete and deformed specimens, both lacking anterior and posterior margins (see Ehiro et al. 2019: fig. 10a–d). Regarding *Kitakamicaris* (Fig. 4G; see Ehiro et al. 2015: figs 4, 5, 8, 9), it was interpreted as being close to *Microcaris* Pinna, 1974 (Middle Triassic of China, Italy and Slovenia; Upper Triassic of Austria and Italy) on the basis of the shape of the shield and on the micro-ornamentation (vertical ridges). The shape is actually more similar to *Ankitokazocaris* (Fig. 4): it bears a triangular-shaped rostrum, a convex dorsal midline, a vertical posterior margin and a round antero-ventral corner. According to Ehiro et al. (2015), the main difference with *Ankitokazocaris* is the micro-ornamentation of the shield, with the presence of vertical ridges in *Kitakamicaris* (Fig. 4G). Microstructures of the cuticle have been considered important characters for the taxonomy of Eucrustacea, as for Decapoda (Waugh & Feldmann 2003) but also for Thylacocephala (Broda et al. 2020). However, such structures might vary according to the sex, the ontogeny or the molting cycle of the organism (Waugh et al. 2009). It can also be affected by the type of preservation. With the reinterpretation of *Parisicaris* as *Ankitokazocaris*, we show

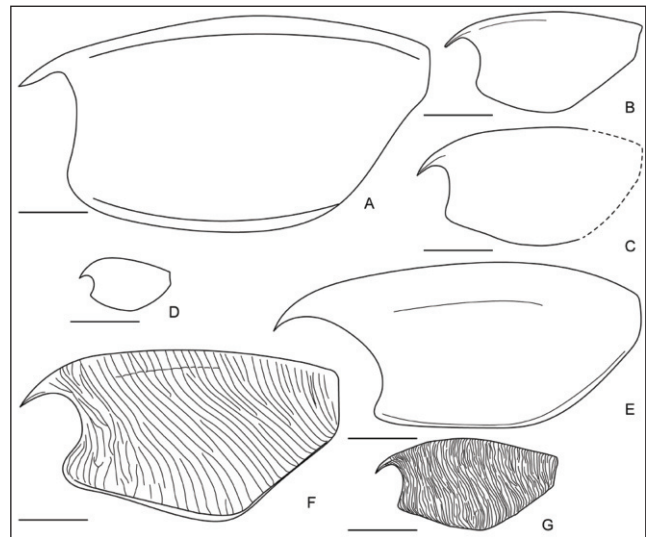


Fig. 4 - Shield morphology among representatives of *Ankitokazocaris*. A: *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar). B, C: *Ankitokazocaris chaobuensis* Ji, Tintori, Jiang & Motani, 2017. B: *Ankitokazocaris chaobuensis* from China (late Spathian, Early Triassic, China); C: *Ankitokazocaris tatensis* Ehiro, Sasaki, Kano & Nagase, 2019 (drawing based on IGPS 111873; junior synonym of *A. chaobuensis*; Japan). D: *Ankitokazocaris parva* (Ehiro, Sasaki, Kano & Nagase 2019) nov. comb. (Spathian, Early Triassic, Japan). E: *Ankitokazocaris bandoi* Ehiro & Kato in Ehiro, Sasaki, Kano, Nemoto & Kato, 2015 (Spathian, Early Triassic, Japan). F: *Ankitokazocaris triassica* (Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019) nov. comb. (early Spathian, Early Triassic, U.S.A.). G: *Ankitokazocaris utatsuensis* (Ehiro & Kato in Ehiro, Sasaki, Kano, Nemoto & Kato 2015) nov. comb. (Spathian, Early Triassic, Japan). Scales: 10 mm.

that specimens of *Ankitokazocaris* can be preserved as a smooth shield, with only few ridges or with a fully ornamented shield. Following Briggs et al. (2015) for the eucrustacea *Iosuperstes collisionis* Briggs, Liu, McKay & Witzke, 2015 from the Winneshiek Lagerstätte, we decided to group shields of similar morphology together in *Ankitokazocaris* and to consider *Kitakamicaris* and *Miyagicaris* as junior synonyms of *Ankitokazocaris* pending further evidences.

Among Palaeozoic taxa, *Concavicaris sinuata* (Meek & Worthen, 1868) from the Carboniferous of U.S.A. has been considered by Schram (2014) to belong to *Ankitokazocaris*. Two other species of *Concavicaris* from the Palaeozoic might fit into *Ankitokazocaris*: *Concavicaris incola* Chlupáč, 1963 from the Devonian of Czech Republic, and *Concavicaris georgeorum* Schram, 1990 from the Carboniferous of Mazon Creek, U.S.A. They have a convex dorsal midline, a short rostrum slightly curved downward and a ventral margin subdivided into short anterior and long posterior parts by sharp angle. However,

they differ slightly from *Ankitokazocaris* representatives by their really short and convex posterior margin and the anterior part of their ventral margin, which is more abruptly inclined, forming a smaller and more convex optic notch. A detailed review of these species is necessary before concluding on their affinities.

Ankitokazocaris acutirostris Arduini, 1990

Figs 4A, 5–8

- 1990 *Ankitokazocaris acutirostris* Arduini, p. 199, figs 2, 3
 2014 *Ankitokazocaris acutirostris* – Schram, p. 350
 2015 *Ankitokazocaris acutirostris* – Ehiro et al., p. 272, 273
 2017 *Ankitokazocaris acutirostris* – Ji et al., p.174
 2019 *Ankitokazocaris acutirostris* – Charbonnier et al., tab. 1
 2019 *Ankitokazocaris acutirostris* – Ehiro et al., p.324, 326

Type material. Holotype MSNM i10836, paratypes MSNM i11038–11064.

Type locality. Ambatolokobè, Ankitokazo Basin, Madagascar.

Type level. Middle Sakamena Formation, Dienerian/Smithian, Early Triassic.

Additional examined material. MNHN.FA72327 from the Middle Sakamena Formation, Ambatolokobè, Ankitokazo Basin, Madagascar (Dienerian/Smithian, Early Triassic).

Emended description. Thylacocephala with a folded shield. No suture is visible in dorsal view. Antero-posterior axis is the longest (see Tab. 2 for measurements). Part and counter-part are preserved in most of the specimens. No trace of trunk, digestive tract or gills are visible.

Shield outline. Shield is subrectangular in lateral view (Figs 5A–D, 8). Anterior margin is formed of a well-developed and asymmetrical concave optic notch (on; Figs 5A–D, 7A, B). Antero-dorsal corner is drawn out as a sharp, short, triangular-shaped rostrum (r; Figs 5A–D, 7A, B). The unarticulated rostrum is directed antero-ventrally.

The dorsal midline (dm) is rectilinear in the anterior third and then gently convex medially (Fig. 5A–D, G, H). It is more curved near the rostrum. Postero-dorsal corner is rounded.

The posterior margin is short (pm), slightly convex and vertical (Fig. 8A, B, E, F). The transition between the posterior and ventral margins is not clearly distinguishable as the postero-ventral corner is rounded.

The ventral margin (vm) is divided into two parts (Fig. 8E, F). The posterior half is steeply descending antero-ventrally. The anterior part is slightly ascending antero-dorsally. The antero-ventral corner is rounded.

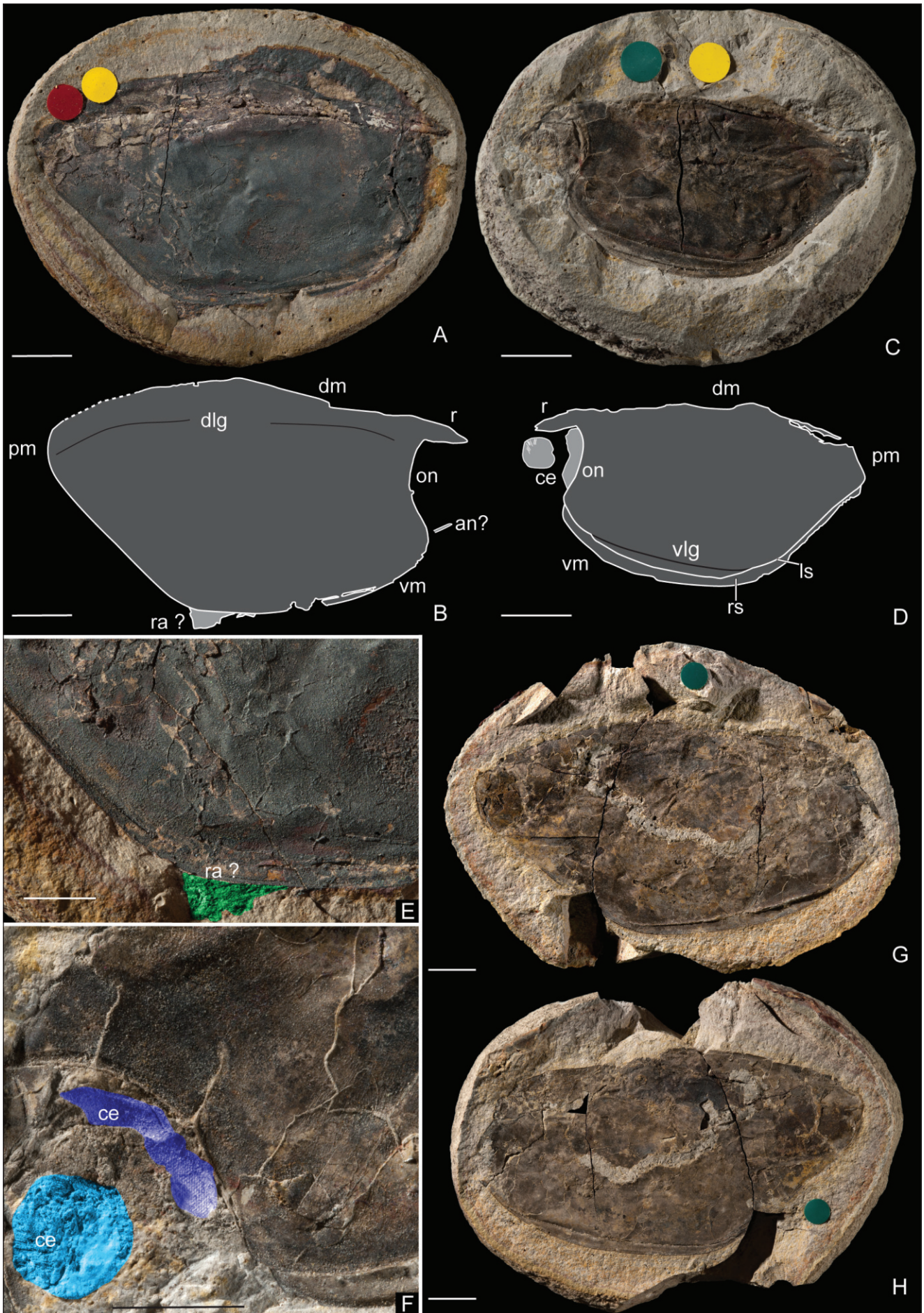
Shield ornamentation. The outer layer of the shield is formed of sinuous, small and thin vertical ridges (Fig. 7E–G). When the outer layer of the shield is broken, it is possible to see a more internal layer of the shield. Small tubercles are observed on this layer. One rounded pore is preserved above the anterior part of the ventral margin (Fig. 6E–G).

A convex, longitudinal groove (dlg) is running from the base of the rostrum to the posterior margin in the dorsal area of the shield (Figs 5A–B, 7A–G). It is parallel to the dorsal midline. A ventro-lateral narrow groove (vlg) starting at the middle of the posterior part of the ventral margin (Figs 5C, D, G, H, 7A–F) and then following the ventral margin anteriorly, delimits a marginal fold.

Sensory structures. Two circular compound eyes are preserved (ce; d = 4.8 mm; Figs 5C, D, F, 7A, B). No stalk is observed. The eye surface is formed of hexagonal structures which are most likely ommatidia (l = 133–191 µm; w = 103–123 µm). In longitudinal section, ommatidia appear as a columnar structure. There are approximately 73 ommatidia per mm².

Cephalic appendages. An antenniform structure is protruding from the convex part of the anterior margin (an?; l = 2.55–3.58 mm). It appears tube-shaped (Figs 5A, B, 6A–D). This possible antennule or antenna is formed of two parts: a larger (w = 0.435 mm) and rectangular posterior part and a thinner anterior part (w = 0.328 mm) that ends in a rounded tip.

Fig. 5 - *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar). A, B, E: holotype MSNM i10836; A: left lateral view; B: line drawing; E: close-up of possible raptorial appendage. C, D, F: MSNM i11040; C: left lateral view; D: line drawing; F: close-up of compound eyes (colour-marked). H: left lateral view of paratype MSNM i11047 (counter-part). I: left lateral view of paratype MSNM i11054 (part). Abbreviations: an?, antenniform structure; ce, compound eye; dlg, dorso-lateral groove; dm, dorsal midline; ls, left side; on, optic notch; pm, posterior margin; r, rostrum; ra?, raptorial appendage?; rs, right side; vlg, ventro-lateral groove; vm, ventral margin. Scales: A–D, G, H, 10 mm; E–F, 5 mm. Photographs: Philippe Loubry. Line drawings: Thomas Laville.



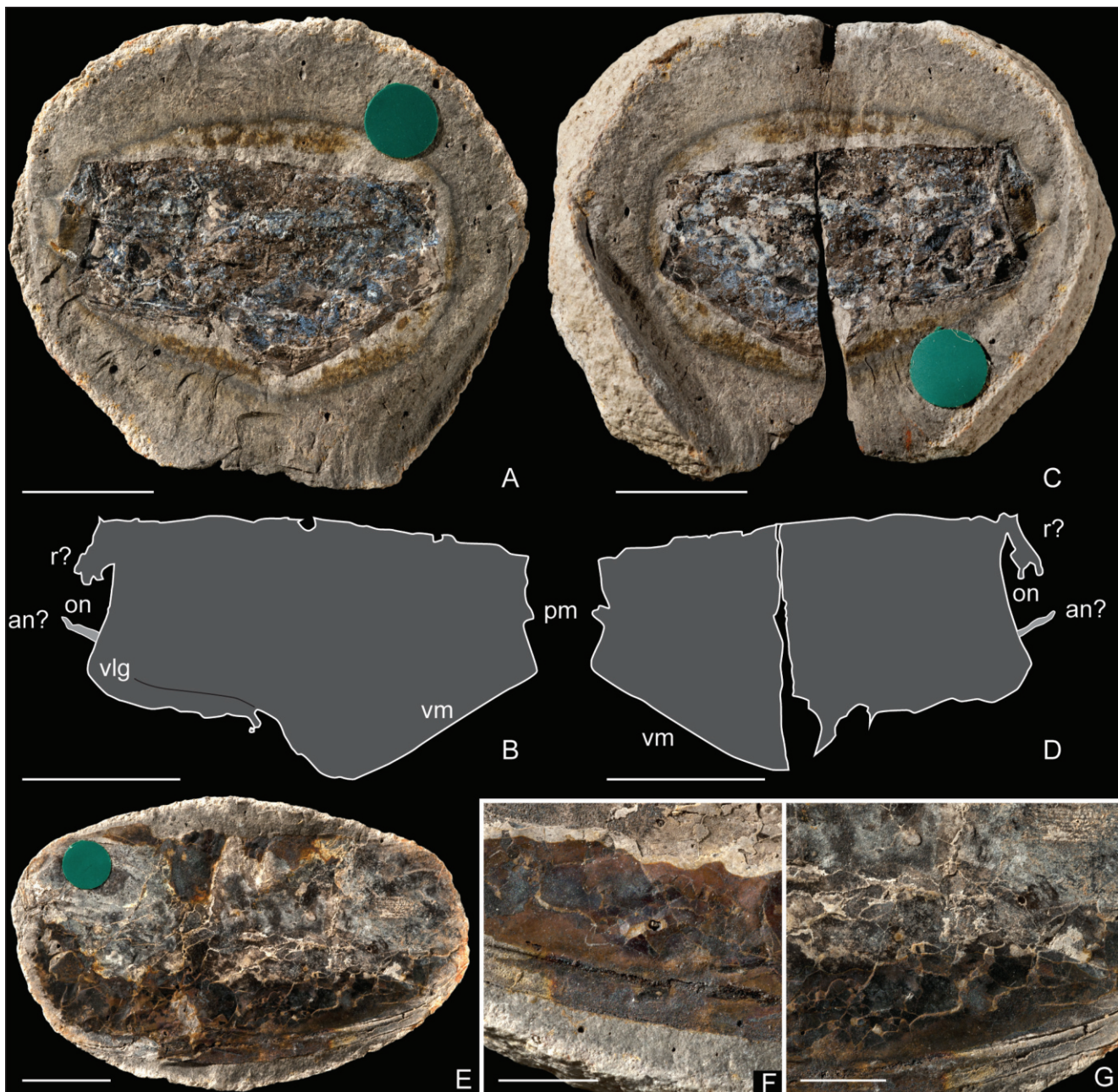


Fig. 6 - *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar). A–D: paratype MSNM i11046; A: left lateral view (part); B: left lateral view (counter-part); C: line drawing (part); D: line drawing (counter-part). E–G: paratype MSNM i11045; E: left lateral view; F, G: close-up of possible pores. Abbreviations: an?, antenniform structure; on, optic notch; pm, posterior margin; r?, rostrum?; vlg, ventro-lateral groove; vm, ventral margin. Scales: A–D, E, 10 mm; F, G, 5 mm. Photographs: Philippe Loubrly. Line drawings: Thomas Laville.

Raptorial appendages. A small part of a possible raptorial appendage (ra?) is emerging from the border between the posterior and medial parts of the ventral margin (Fig. 5A, B, E).

Muscles. In a broken specimen, radial structures are conserved which might be adductor muscles of the shield (Fig. 8E, F).

Ankitokazocaris chaohuensis Ji, Tintori, Jiang & Motani, 2017

Fig. 4B, C

2017 *Ankitokazocaris chaohuensis* Ji, Tintori, Jiang & Motani, p. 175, fig. 3, 5–8

2019 *Ankitokazocaris chaohuensis* – Charbonnier et al., tab. 1

2019 *Ankitokazocaris chaohuensis* – Ehiro et al., p. 324

2019 *Ankitokazocaris tatensis* Ehiro, Sasaki, Kano & Nagase, p. 324, fig. 6

Type material. Holotype NIGP 163032, paratypes NIGP 163033–163060.

Type locality. Majiashan Quarry, Chaohu, Hefei City, Anhui Province, PR China.

Type level. Upper member of Nanlinghu Formation, late Spathian, late Olenekian, Early Triassic.

Additional material. IGPS 111873–111875; UIM 30625–30626. All additional specimens are from the middle part of the Osawa Formation (Spathian, late Olenekian, Early Triassic), north of Cape Tatezaki, Utatsu, Minamisanriku Town, Miyagi Prefecture, Northeast Japan.

Emended diagnosis. *Ankitokazocaris* species up to 32 mm in total length. Shield with a concave and asymmetrical optic notch; rostrum well-developed and gently curved antero-ventrally; slightly convex dorsal midline; anterior and posterior part of the ventral margin nearly equal in length, forming an angle of 125–145°; posterior margin short and nearly vertical, without posterior spine; presence of a dorso-lateral carina starting from the rostrum, parallel to the dorsal midline; eyes large, with small ommatidia (about 100/mm²), apparently not stalked; at least 14 posterior appendages; raptorial appendages large, extending ventrally from the shield.

Remarks. Ehiro et al. (2019: p.324, fig. 6) erected *Ankitokazocaris tatensis* based on specimens from the Osawa Formation, northeast Japan (late Olenekian). This species shared multiple characters with *Ankitokazocaris chaobuensis* (Ji et al 2017: p.175, figs 3, 5–8): size, optic notch well-developed and asymmetrical, rostrum gently curved antero-ventrally, ventral margin divided into two parts with a posterior half steeply descending antero-ventrally and an anterior part, slightly ascending antero-dorsally (Fig. 4C, G). However, Ehiro et al. (2019) provided differences between *A. tatensis* and *A. chaobuensis*. They assumed variation in the general morphology of the shield in lateral view (trapezoidal/triangular), of the antero-ventral corner (both are rounded) and in ornamentation (presence or absence of lateral carina). The differences in the general morphology of the shield is only a semantic issue, both shields having a trapezoidal shape in lateral view. Specimens of *A. chaobuensis* also have a dorso-lateral carina (NIGP163032, 163046; see Ji et al. 2017: figs 3b, 5g). Thus, we consider *Ankitokazocaris tatensis* as a junior synonym of *Ankitokazocaris chaobuensis*.

***Ankitokazocaris parva* (Ehiro, Sasaki, Kano & Nagase, 2019) nov. comb.**

Fig. 4D

2019 *Concavicularis parva* Ehiro, Sasaki, Kano & Nagase, p. 327, figs 7-9

Type material. Holotype IGPS 111876, paratypes IGPS 111877–111882; paratypes UIM 30627–30628.

Type locality. North of Cape Tatezaki, Utatsu, Minamisanriku Town, Miyagi Prefecture, northeast Japan.

Type level. Middle part of the Osawa Formation, Spathian, late Olenekian, Early Triassic.

Emended diagnosis. *Ankitokazocaris* having a semi-oval shield in lateral view with a strongly curved downward rostrum and a convex ventral margin; densely distributed small pits on the whole shield surface.

Remarks. The present review of the specimens of *A. parva* has indicated that the large optic notch, the sharp anterior rostrum, the convex dorsal midline, the short and vertical posterior margin and the ventral margin subdivided into anterior and posterior parts are diagnostic characters of *Ankitokazocaris* and thus we propose the new combination *Ankitokazocaris parva* nov. comb. *Ankitokazocaris parva* differs from other *Ankitokazocaris* species by its short, strongly curved rostrum and its more convex ventral margin (Fig. 4B). As mentioned by Ehiro et al. (2019), *Ankitokazocaris parva* (Ehiro, Sasaki, Kano & Nagase, 2019) has a similar morphology as *Concavicularis sinuata*: they only differ by their size, the straight dorsal midline and the presence of small pits in *C. parva*. According to Broda et al. (2020), it is probable that such pores are not preserved or visible in *C. sinuata*.

One striking feature for *Ankitokazocaris parva* is its small size compared to other thylacocephalan representatives from the Early Triassic of Japan. It might represent a juvenile stage of another *Ankitokazocaris* species. Knowledge on the ontogeny of thylacocephalans is highly restricted. Size differences have been reported for *Dollocaris ingens* from the Middle Jurassic of France: it ranges from 27 mm to 300 mm (Secrétan & Riou 1983; Charbonnier et al. 2009). A true juvenile stage has only been reported once, for *Concavicularis milesi* Briggs & Rolfe, 1983 from the Devonian of Australia. For this taxa, morphological differences were noticed with variation in the morphology of the optic notch and the posterior margin in addition to size difference. Given the few specimens available for *Ankitokazocaris parva*, we cannot firmly conclude on those specimens representing a juvenile stage of another *Ankitokazocaris* species from the Early Triassic of Japan.

***Ankitokazocaris triassica* (Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019) nov. comb.**

Figs 4F, 9, 10

2019 *Parisicaris triassica* Charbonnier in Charbonnier, Brayard & the Paris Biota team, figs 2, 3

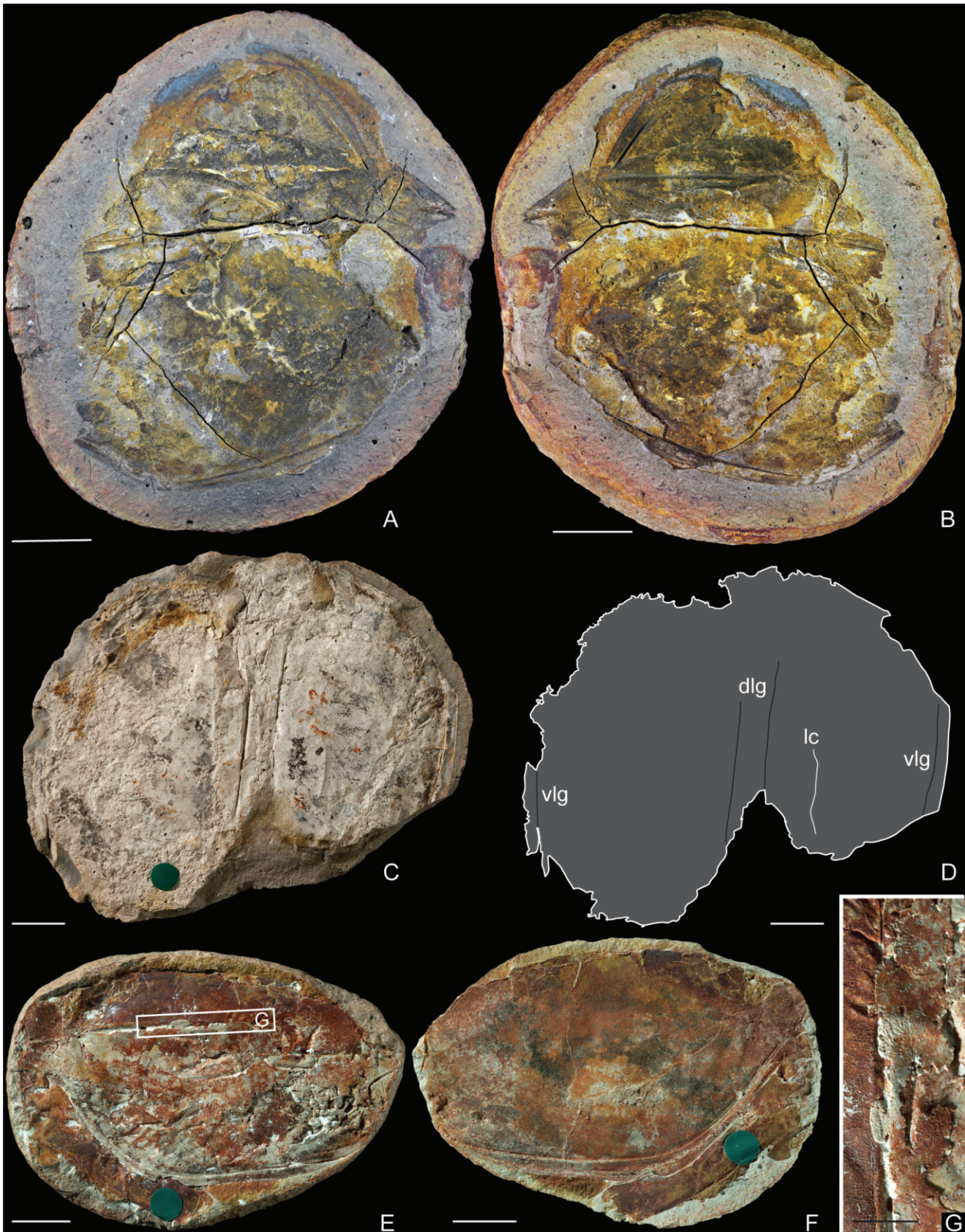


Fig. 7 - *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar). A, B: MNHN.FA72327; A: dorsal view (counter-part); B: dorsal view (part). C, D: paratype MSNM i11053; C: dorsal view; D: line drawing. E–G: paratype MSNM i11044; E: left-lateral view (counter-part); F: left-lateral view (part); G: close-up of micro-ornamentation. Abbreviations: dlg, dorso-lateral groove; lc, lateral carina; vlg, ventro-lateral groove. Scales: A–F, 10 mm; G, 5 mm. Photographs: A, B, Thomas Laville; C, E–G, Philippe Loubry. Line drawing: Thomas Laville.

Tab. 2 - Summary of descriptive statistics (measurements). Abbreviations: Aad, antero-dorsal angle; Aav, antero-ventral angle; Apd, postero-dorsal angle; Apv, postero-ventral angle; ha, anterior shield height; hmax, maximal shield height; hp, posterior shield height; lr, length of the rostrum; ls, length of the shield; lw, length without rostrum.

	<i>A. acutirostris</i> (N=7)	<i>A. triassica</i> (N=6)	<i>L. parisiana</i> (N=7)	<i>O. ambatolokobensis</i> (N=3)
ls (mm)				
Mean (SD)	58.21 (15.51)	45.20 (5.78)	18.11 (9.86)	45.82 (6.06)
Median	58.21	45.23	15.80	47.97
Range	47.24 - 69.18	39.41 - 50.96	8.81 - 32.05	38.98 - 50.51
lw (mm)				
Mean (SD)	61.08 (14.49)	40.19 (5.38)	15.87 (8.14)	NA
Median	61.32	40.82	14.10	NA
Range	43.10 - 78.57	34.52 - 45.23	8.00 - 27.28	NA
lr (mm)				
Mean (SD)	6.54 (1.56)	4.25 (1.68)	2.35 (1.07)	NA
Median	5.94	4.67	2.46	NA
Range	5.36 - 8.31	1.86 - 5.80	0.82 - 3.60	NA
ha (mm)				
Mean (SD)	19.59 (4.18)	12.58 (5.75)	6.47 (2.25)	22.41 (2.32)
Median	19.42	12.56	6.53	23.31
Range	14.79 - 24.73	7.58 - 17.61	2.63 - 9.18	19.78 - 24.15
hmax (mm)				
Mean (SD)	38.32 (7.56)	22.55 (8.21)	9.05 (3.77)	26.62 (2.73)
Median	38.83	25.66	7.77	26.35
Range	24.73 - 47.78	10.48 - 28.39	4.00 - 13.56	24.04 - 29.47
hp (mm)				
Mean (SD)	10.73 (2.51)	8.06 (2.69)	2.55 (0.82)	8.83 (3.32)
Median	11.15	8.76	2.75	8.55
Range	6.58 - 13.06	3.68 - 10.51	1.20 - 3.28	5.66 - 12.29
Aad (degree)				
Mean (SD)	86.32 (10.84)	67.46 (18.98)	49.81 (11.40)	64.34 (5.83)
Median	91.18	58.29	53.44	65.44
Range	73.90 - 93.89	48.90 - 90.78	32.23 - 61.26	58.04 - 69.54
Aav (degree)				
Mean (SD)	115.43 (2.02)	83.73 (13.87)	93.06 (19.44)	66.27 (1.59)
Median	115.15	81.30	96.50	65.57
Range	113.78 - 118.75	71.62 - 100.72	58.88 - 111.86	65.16 - 68.09
Apv (degree)				
Mean (SD)	148.11 (4.92)	118.85 (6.79)	92.76 (33.13)	92.93 (3.10)
Median	150.78	117.81	85.91	91.45
Range	141.27 - 152.93	109.63 - 127.95	60.22 - 139.00	90.85 - 96.50
Apd (degree)				
Mean (SD)	105.98 (5.02)	119.57 (12.09)	140.70 (8.03)	86.01 (7.69)
Median	103.93	123.35	139.50	84.03
Range	100.83 - 113.08	105.72 - 134.64	133.67 - 150.15	79.50 - 94.50
hmax/ls				
Mean (SD)	0.54 (0.03)	0.59 (0.03)	0.46 (0.04)	0.58 (0.06)
Median	0.54	0.59	0.46	0.61
Range	0.52 - 0.56	0.56 - 0.62	0.42 - 0.50	0.52 - 0.62

Type material. Holotype UBGD 30561, paratypes UBGD 30614, 30615.

Type locality. Paris Canyon, west of the Paris city, Bear Lake County, Idaho, U.S.A.

Type level. Early Spathian, late Olenekian, Early Triassic.

Additional examined material. UBGD 32321, UBGD 32322 from Georgetown, Idaho, U.S.A (early Spathian, Early Triassic); IMNH 288/1701, IMNH 288/1702 from Stewart Canyon, Idaho, U.S.A (early Spathian, Early Triassic).

Emended description. Thylacocephala with a folded shield. Antero-posterior axis is the longest (Tab. 2). All specimens are preserved in lateral view. No trace of raptorial appendages, digestive tract or gills are visible.

Shield outline. Shield is subrectangular in lateral view (Figs 9, 10). Anterior margin is formed of a broadly excavated, concave optic notch (on) dorsally. Antero-dorsal corner is drawn out as a small, sharp, triangular-shaped rostrum (r; Figs 9, 10A, D). The unarticulated rostrum is inclined ventrally. It is fused with the shield. The dorsal midline (dm) is convex, regular (i.e., without crest). Postero-dorsal corner is sharp. The posterior margin (pm) is short, straight and vertical. The postero-ventral corner is rounded. The ventral margin (vm) is convex and divided in two parts. The posterior half is straight, steeply descending antero-ventrally. The anterior

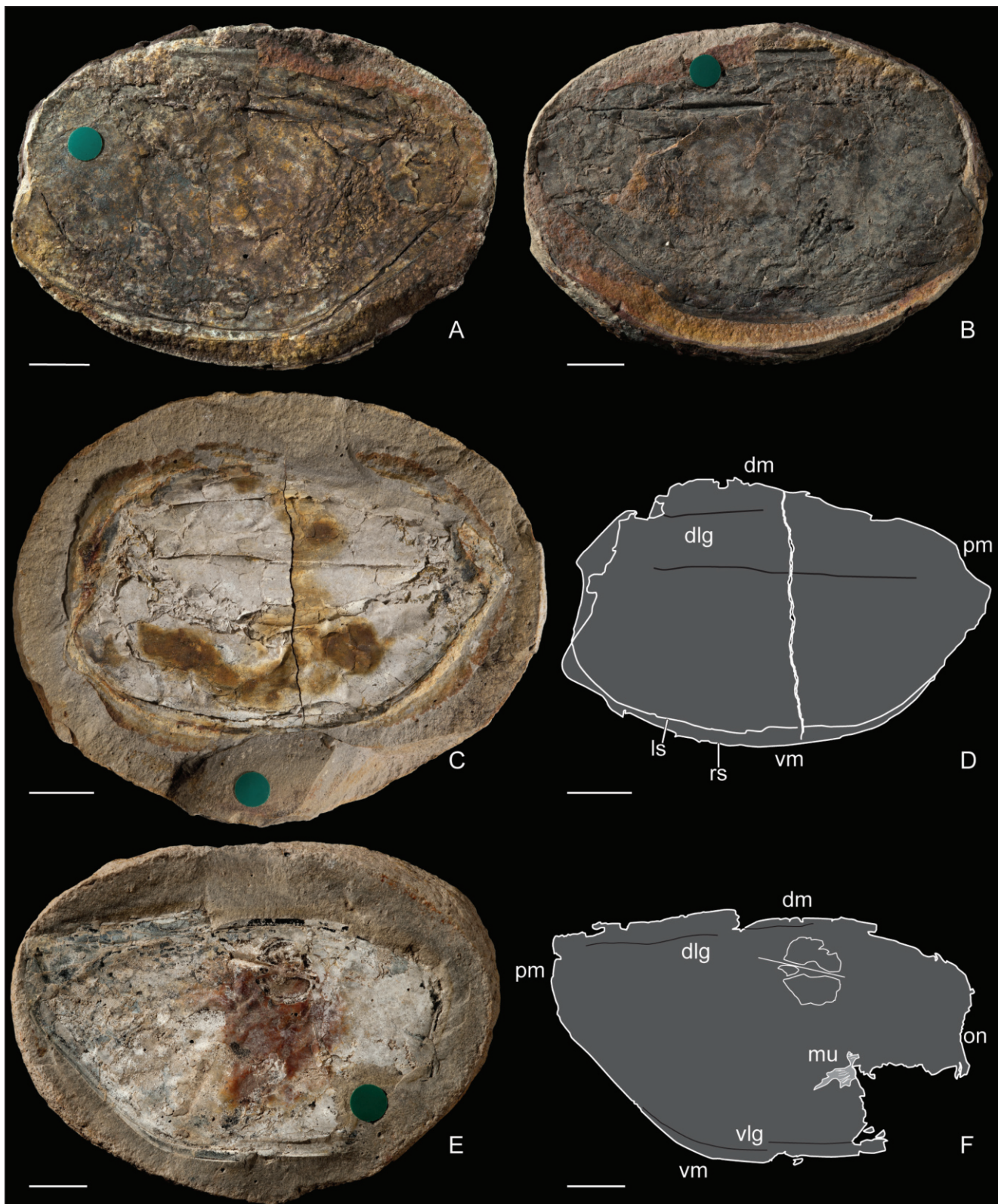


Fig. 8 - *Ankitokazocaris acutirostris* Arduini, 1990 (Dienerian/Smithian, Early Triassic, Madagascar). A, B: paratype MSNM i11038; A: right-lateral view (counter-part); B: right-lateral view (part). C, D: paratype MSNM i11048; C: right-lateral view; D: line drawing. E, F: paratype MSNM i11058; E: right-lateral view; F: line drawing. Abbreviations: dlg, dorso-lateral groove; dm, dorsal midline; ls, left side; mu, radially arranged muscles; pm, posterior margin; rs, right side; vm, ventral margin. Scales: 10 mm. Photographs: Philippe Loubry. Line drawings: Thomas Laville.

part is slightly ascending antero-dorsally. The antero-ventral corner is rounded. The ventral margin is

thicker than the rest of the shield, forming a marginal fold.

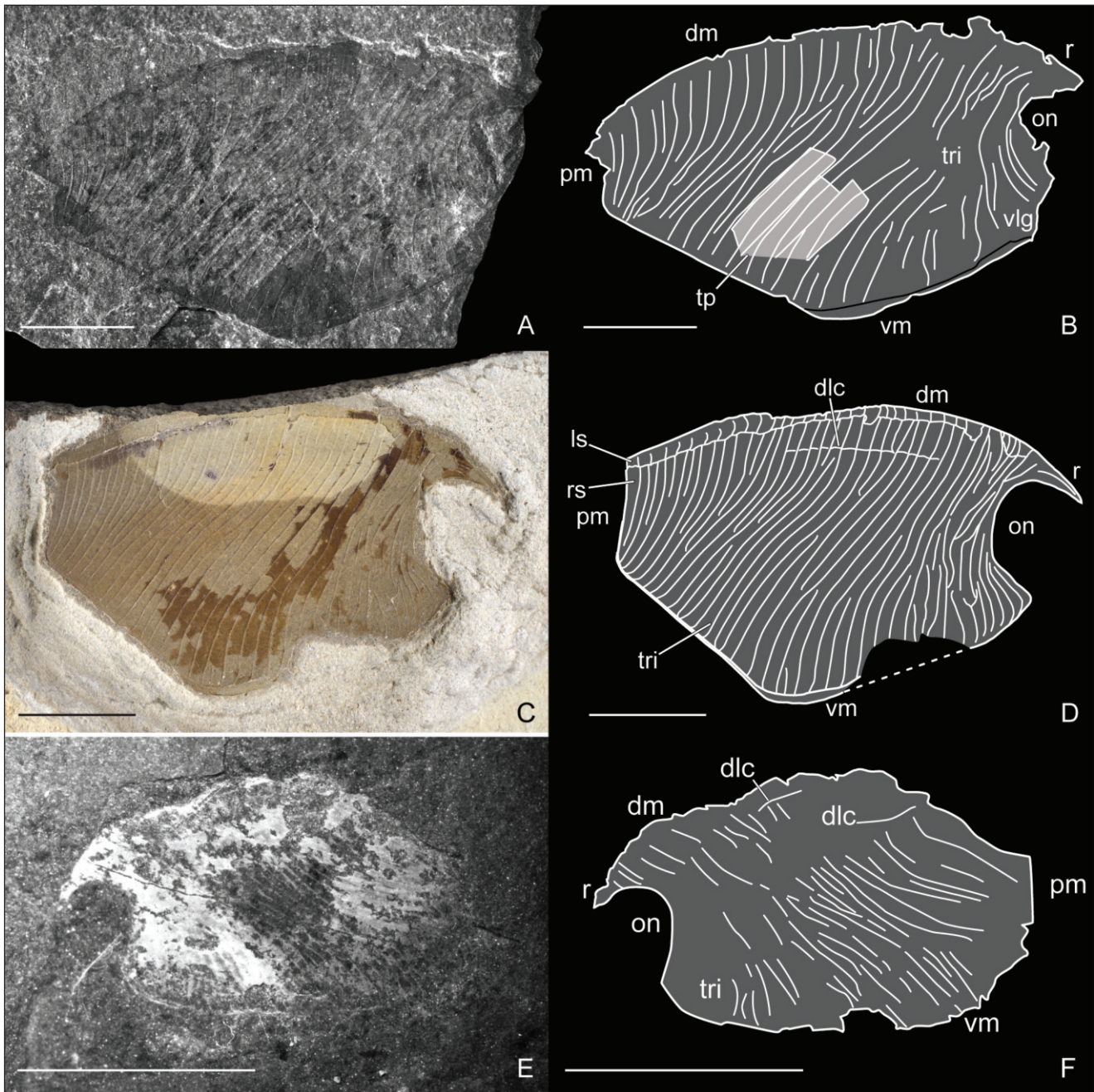


Fig. 9 - *Ankitokazocaris triassica* (Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019; early Spathian, Early Triassic, U.S.A.). A, B: IMNH 288/1702; A: right-lateral view (composite; transmission filters: 400, 500, 600, 650 nm; emission filter: 650 nm); B: line drawing. C, D: holotype UBGD 30561. C: right-lateral view; D: line drawing. E, F: UBGD 32322; E: left-lateral view (composite; transmission filters: 405, 460, 525, 580 nm; emission filters: 650, 792 nm); F: line drawing. Abbreviations: dlc, dorso-lateral carina; dm, dorsal midline; ls, left side; on, optic notch; posterior margin; r, rostrum; rs, right side; tp, trunk pleurites; tri, transversal ridges; vlg, ventro-lateral groove; vm, ventral margin. Scales: A, D, E, 10 mm; B, 5 mm; C, 0.5 mm. Photographs: A, Thomas Laville. C, E, Christopher Smith. Line drawings: B, D, Thomas Laville; F, Sylvain Charbonnier.

Shield ornamentation. The shield is formed of falciform, transversal ridges oriented postero-ventrally (tri; Figs 9, 10). Twenty primary ridges are running parallel to each other from the dorsal midline to the ventral margin. Secondary ridges are inserted sporadically in both dorsal (ca. 12 ribs) and ventral (ca. 12 ribs) areas, most of them being interrupted

before reaching the middle of the shield. Close to the dorsal midline, ridges are almost vertical. They become more inclined ventrally. Most of the ridges are running along the whole shield. Near the anterior margin, ridges are parallel to this margin, following its change in orientation.

A convex, longitudinal carina is running from

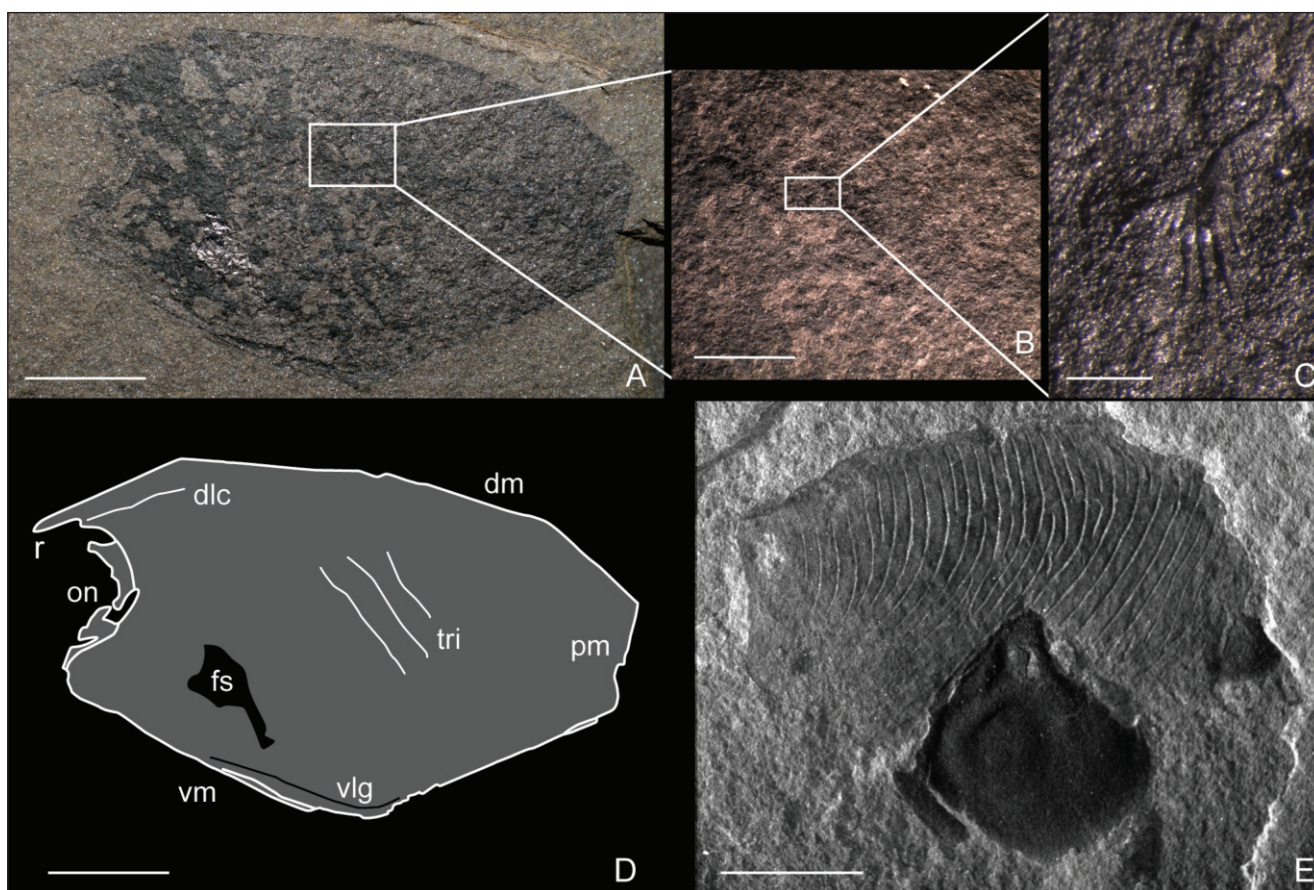


Fig. 10 - *Ankitokazocaris triassica* (Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019; early Spathian, Early Triassic, U.S.A.). A–D: IMNH 288/1701; A: left-lateral view; B: close-up on the central area of the shield; C: close-up on the Gondolellidae S0 element; D: line drawing. E: UBGD 32321 (composite; transmission filters: 400, 600 nm; emission filters: 571, 650 nm). Abbreviations: dlc, dorso-lateral carina; dm, dorsal midline; fs, fish scale; on, optic notch; pm, posterior margin; r, rostrum; tri, transversal ridges; vlg, ventro-lateral groove; vm, ventral margin. Scales: 10 mm. Photographs: Christopher Smith. Line drawing: Thomas Laville.

the base of the rostrum to the centre of the shield on its dorsal area (dlc; Figs 9C–F, 10A, D). It is parallel to the dorsal midline. A ventro-lateral narrow groove (vlg) starting at the middle of the posterior part of the ventral margin (Fig. 9) follows the ventral margin anteriorly, delimiting the marginal fold.

In the central area of the shield, a conodont element can be observed (Fig. 10A–C).

Trunk. Three rectangular, elongated trunk pleurites are preserved in the posterior area of the shield (tp; Fig. 9A, B).

Remarks. New observations indicate that *Parisicaris triassica* has the general morphology of *Ankitokazocaris*: a sharp, triangular-shaped rostrum, a gently convex dorsal midline, a short posterior margin and an anterior margin divided in a dorsal, well-developed optic notch and a convex ventral part. Thus, we proposed the new combination *Ankitokazocaris triassica* (Charbonnier in Charbonnier et al., 2019) nov. comb.

Ankitokazocaris triassica differs from *A. acutirostris*, the type species, which has a convex dorsal midline, rectilinear in the anterior third. No transversal ridges were found in *A. acutirostris*.

Compared to *A. triassica*, *Ankitokazocaris chaobuensis* has a long rostrum. Its anterior margin is formed of a well-developed optic notch but the ventral part of the margin is not clearly convex. Only the antero-ventral corner is rounded.

Ankitokazocaris triassica has similar vertical ridges as *Ankitokazocaris utatsuensis* (Ehiro & Kato in Ehiro et al., 2015). However, it bears less ridges which are more spaced. Its anterior margin is also symmetrical and more concave than the one from *A. utatsuensis*. Its anterior margin is postero-ventrally oriented while it is antero-ventrally oriented in *A. triassica*. No dorso-lateral carina in the central area of the shield nor a ventro-lateral groove are present in *A. utatsuensis*.

Ankitokazocaris utatsuensis (Ehiro & Kato in Ehiro, Sasaki, Kano, Nemoto & Kato, 2015)
nov. comb.

Fig. 4G

2015 *Kitakamicaris utatsuensis* Ehiro & Kato in Ehiro, Sasaki, Kano, Nemoto & Kato, p. 274, figs 4, 5, 7–9

2019 *Kitakamicaris utatsuensis* – Charbonnier et al., p. 42

2019 *Kitakamicaris utatsuensis* – Ehiro et al., p. 323

2019 *Miyagicaris costata* Ehiro, Sasaki, Kano & Nagase, p. 329, fig. 10

Type material. Holotype IGPS 111448, paratypes IGPS 111449–111495, 111497; paratypes UIM 30604–30610.

Type locality. North of Cape Tatezaki, Utatsu, Minamisanriku Town, Miyagi Prefecture, northeast Japan.

Type level. Middle part of the Osawa Formation, Spathian, late Olenekian, Early Triassic.

Additional examined material. IGPS 111883; UIM 30629. All additional specimens are from the middle part of the Osawa Formation (Spathian, late Olenekian), north of Cape Tatezaki, Utatsu, Minamisanriku Town, Miyagi Prefecture, northeast Japan.

Original diagnosis (repeated from Ehiro et al. 2015) – Trapezoidal carapace is longer than it is high and has remarkable vertical ribs on it. The carinated dorsal midline is broadly convex. The ventral margin bends in the central part and is connected with the concave anterior margin at almost a right corner. The rostrum is distinct with central and lateral carinae.

Remarks. *Kitakamicaris utatsuensis* was described based on its vertical ridges. New observations made on *Ankitokazocaris triassica* proved that vertical ridges can also be observed on the shield of representatives of *Ankitokazocaris*. The specimens of *Kitakamicaris utatsuensis* have a general morphology diagnostic of *Ankitokazocaris*: a well-developed optic notch, a sharp, triangular-shaped rostrum, a gently convex dorsal midline, a short and straight posterior margin and a convex ventral part. We therefore propose the new combination *Ankitokazocaris utatsuensis* (Ehiro & Kato in Ehiro et al., 2015) nov. comb.

Miyagicaris costata was described based on deformed and broken specimens by Ehiro et al. (2019: fig. 10a–d). The anterior and posterior margins are missing. Ehiro et al. (2019) distinguished it from *Ankitokazocaris utatsuensis* based on the dendritic branching of the ridges and on the acute antero-ventral corner. The dendritic arrangement is not clear: the deformation and the multiple fractures probably interfere with the original ornamentation pattern. Such deformation can also explain the difference in the antero-ventral angle measurement. Ehiro et al. (2019) highlighted the size difference between both taxa. The length of the shield of *Ankitokazocaris utatsuensis* ranges from 17 to 35

mm while *Miyagicaris costata* reach a larger size (ca. 70 mm). Such amplitude in size is not uncommon in representatives of Thylacocephala. *Concavicaris glenisteri* Briggs & Rolfe, 1983 ranges from 20 to 60 mm or *Concavicaris playfordi* Briggs & Rolfe, 1983 from 15 to 70 mm. The most important known amplitude in length is probably for *Dollocaris ingens*, previously mentioned in this article. *Miyagicaris costata* should then be regarded as a junior synonym of *Ankitokazocaris utatsuensis*.

Ankitokazocaris utatsuensis resembles *Ankitokazocaris chaobuensis* based on similar shield shape and size range. However, *A. chaobuensis* does not bear any vertical ridges. *A. utatsuensis* differs from *Ankitokazocaris acutirostris*, which has a smooth shield, an anterior margin divided into two parts, and a dorsal midline rectilinear in its first third and then convex towards the posterior margin.

Ligulacaris Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019

Type species. *Ligulacaris parisiana* Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019 by monotypy.

Ligulacaris parisiana Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019

Fig. 11

Type material. Holotype UBGD 30562, paratype UBGD 30616.

Type locality. Paris Canyon, west of the Paris city, Bear Lake County, Idaho, U.S.A.

Type level. Early Spathian, late Olenekian, Early Triassic.

Additional examined material. UBGD 32323 from Georgetown, Idaho, U.S.A (early Spathian, Early Triassic); UBGD 32324 from northeastern Nevada, U.S.A (early Spathian, Early Triassic); UBGD 32325 a & b, UBGD 32326, UBGD 32327 from Paris canyon, Idaho, U.S.A (early Spathian, Early Triassic).

Description. Thylacocephala with a folded shield. Antero-posterior axis is the longest (Tab. 1). Specimens are preserved in lateral view. No trace of raptorial appendages, digestive tract or gills are visible.

Shield outline. Shield is oval in lateral view. Anterior margin is formed of a broadly excavated concave optic notch (on). Antero-dorsal corner is drawn out as a small sharp triangular shaped rostrum (r; Fig. 11 A–C, E, F). The unarticulated rostrum is directed anteriorly. The dorsal midline (dm) is slight-

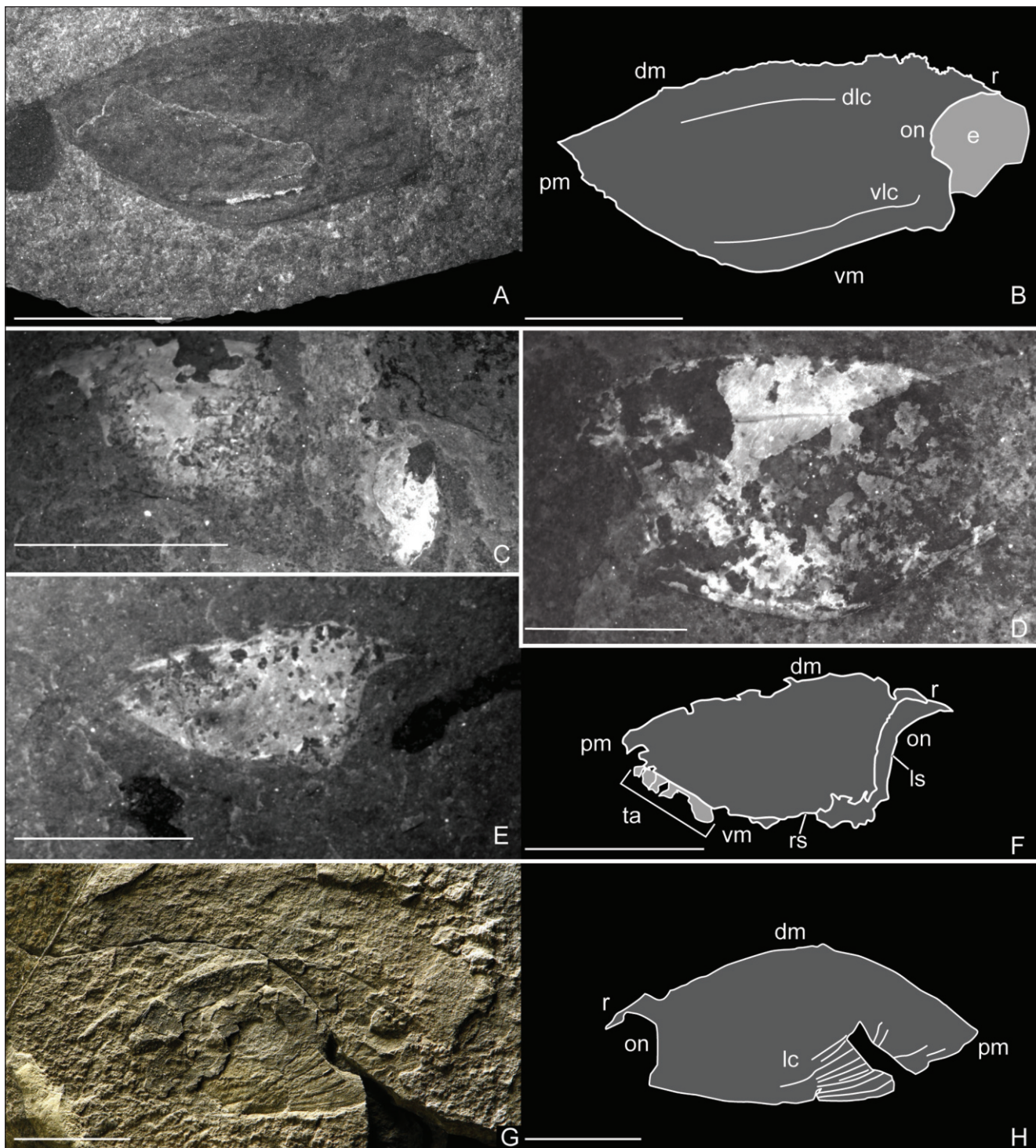


Fig. 11 - *Ligulacaris parisiensis* Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019 (early Spathian, Early Triassic, U.S.A). A, B: UBGD 32323 (composite; transmission filters: 400, 500, 600, 650 nm; emission filter: 650 nm); A: right-lateral view; B: line drawing. C: left lateral view of UBGD 32325'b (composite; transmission filter: 405, 460, 580 nm; emission filter: 650 nm). D: left-lateral view of UBGD 32325'a (composite; transmission filters: 405, 460, 580 nm; emission filter: 650 nm). E, F: UBGD 32327. E: right-lateral view (composite; transmission filters: 405, 460, 580 nm; emission filter: 650 nm); F: line drawing. G, H: UBGD 32324; G: left-lateral view; H: line drawing. Abbreviations: dlc, dorso-lateral carina; dm, dorsal midline; e, eyes; ls, left side; on, optic notch; pds, postero-dorsal spine; pm, posterior margin; r, rostrum; rs, right side; ta, trunk appendages; vlc, ventro-lateral carina; vm, ventral margin. Scales: A, B, D-F, 5 mm; C, G, H, 10 mm. Photographs: Christopher Smith. Line drawings: Thomas Laville.

ly convex and regular. The dorsal midline is more inclined near the rostrum. Postero-dorsal corner is sharp, forming a small spine (pds). The posterior

margin (pm) is short, slightly concave and subvertical. Postero-ventral corner is rounded. The ventral margin (vm) is convex and divided in two parts. The

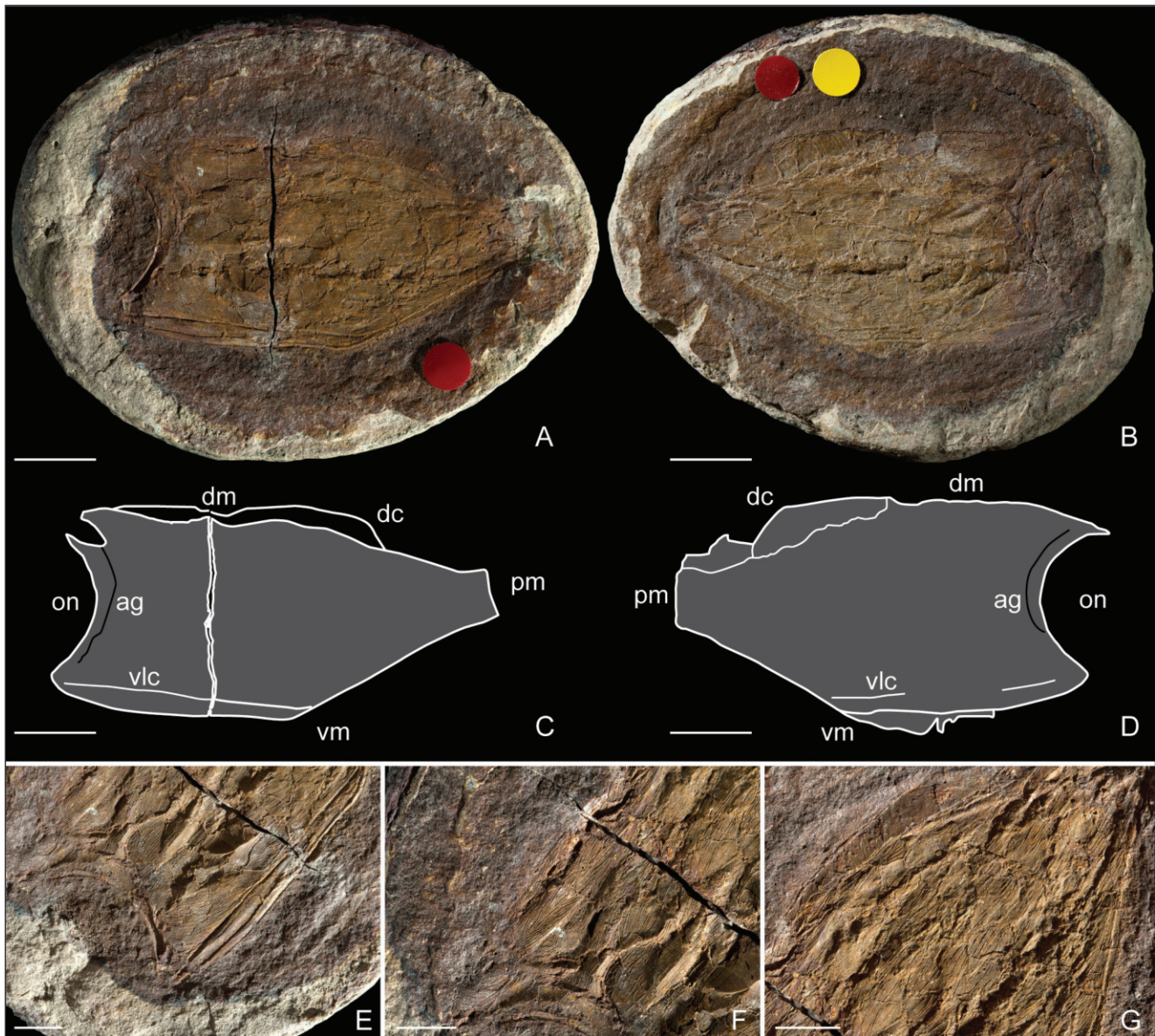


Fig. 12 - *Paraostenia ambatolokobensis* (Arduini, 1990; Dienerian/Smithian, Early Triassic, Madagascar). A–G: holotype MSNM i11037; A: left-lateral view (part); B: left-lateral view (counter-part); C: line drawing (part); D: line drawing (counter-part); E: close-up of antero-ventral area (part); F: close-up of antero-dorsal area (part); G: close-up of dorsal carina. Abbreviations: ag, anterior groove; dc, dorsal carina; dm, dorsal midline; on, optic notch; pm, posterior margin; vlc, ventro-lateral carina; vm, ventral margin. Scales: A–D, 10 mm; F–G, 1 mm. Photographs: Philippe Loubry. Line drawings: Thomas Laville.

posterior half is straight, steeply descending antero-ventrally while the anterior half is horizontal. The antero-ventral corner is rounded. The ventral margin is thicker than the rest of the shield, forming a marginal fold.

Shield ornamentation. A long and convex longitudinal carina is running in the dorso-central area of the shield (dlc; Fig. 11A, B, D). A series of nine longitudinal carinae are visible in the ventral part of the shield (vlc; Fig. 11A, B, G, H). They appear to follow the orientation of the ventral margin: the posterior part steeply descending antero-ventrally

and the anterior part being horizontal.

Sensory structures. Rounded hypertrophied eyes (e) protrude from the optic notch (Fig. 11A, B). Eyes fill almost the entire optic notch.

Trunk appendages. At least five rectangular trunk appendages (ta) protrude from the posterior part of the ventral margin (Fig. 11E, F).

Remarks. Charbonnier et al. (2019: fig. 4a-c) already noticed a series of five longitudinal carinae in the central area of the shield. In UBGD 32324 (Fig. 11G, H), the series of nine longitudinal carinae is located in a more posterior and ventral area.

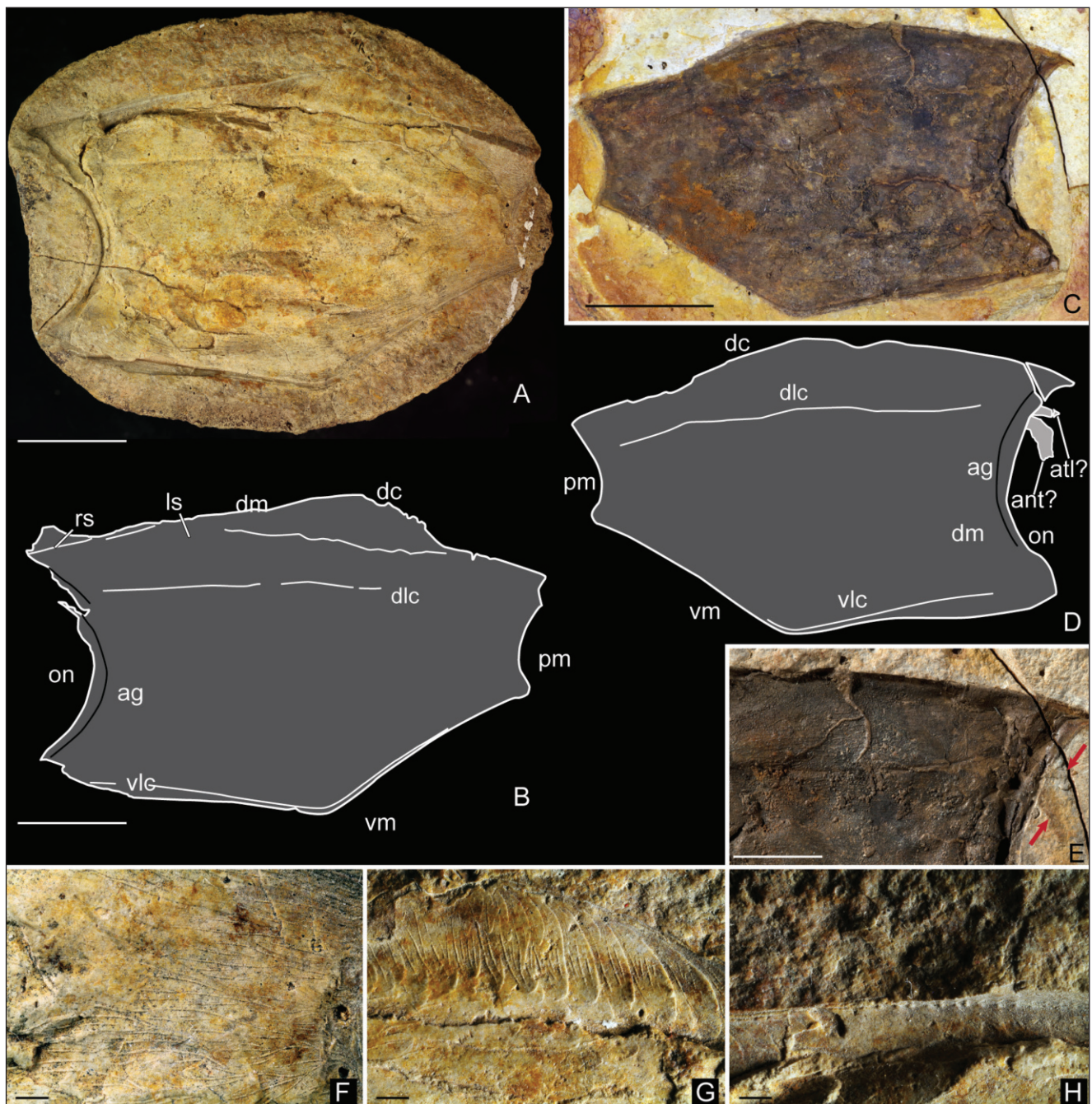


Fig. 13 - *Paraostenia ambatolokobensis* (Arduini, 1990; Dienerian/Smithian, Early Triassic, Madagascar). A, B, F-H: MNHN.FA72326; A: right-lateral view; B: line drawing; F: close-up of furrows; G: close-up of dorsal carina; H: close-up of dorsal midline; C-E: paratype MSNM i19509; C: right-lateral view; D: line drawing; E: close-up on antenniform structures (indicated by the arrows). Abbreviations: ag, anterior groove; ant?, possible antenna; atl?, possible antennula; dc, dorsal carina; dlc, dorso-lateral carina; dm, dorsal midline; ls, left side; on, optic notch; pm, posterior margin; rs, right side; vl, ventro-lateral carina; vm, ventral margin. Scales: A-D, 10 mm; E, 5 mm; F-H, 1 mm. Photographs: A, E, Philippe Loubry; C, Giorgio Teruzzi; F-H, Thomas Laville. Line drawings: Thomas Laville.

It seems likely that the whole shield was covered with such longitudinal carinae.

Paraostenia Secrétan, 1985

Type species. *Paraostenia vultensis* Secrétan, 1985 (Callovi-an, Middle Jurassic, France) by monotypy.

Included species. *Paraostenia ambatolokobensis* (Arduini,

1990), Dienerian/Smithian, Early Triassic, Madagascar – *Paraostenia* sp. (see. Ehiro et al. 2015), Spathian, Early Triassic, Japan

Emended diagnosis. The voluminous and rounded eyes, the gills and the anterior and posterior appendages are as in *Dollocaris*. The form of the carapace is nearly identical to that of *Ostenocaris* pro *Ostenia* (Arduini et al. 1980 amend Arduini et al. 1984) differing in form from *Dollocaris* in the outline which is proportionally higher and shorter and devoid of suborbital spine below the orbital opening which is less deep and more gaping.

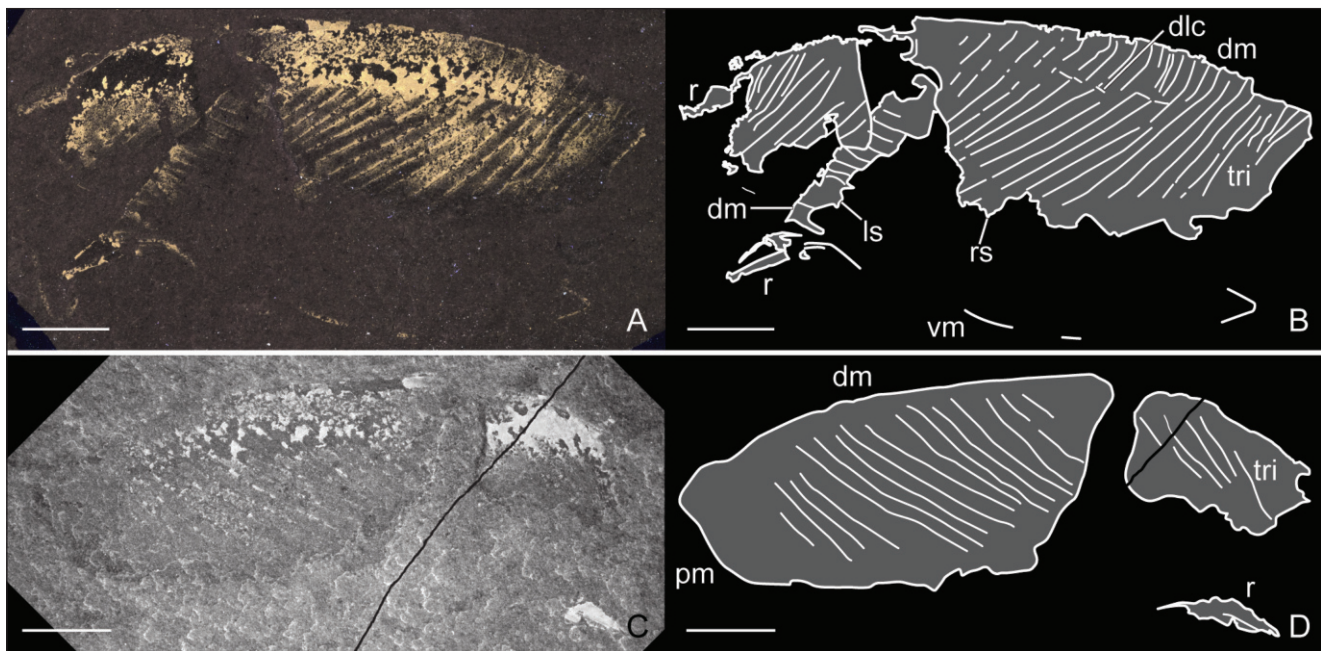


Fig. 14 - Thylacocephala indet (UBGD 30613, former paratype of *Ligulacaris parisiana* Charbonnier in Charbonnier, Brayard & the Paris Biota team, 2019; early Spathian, Early Triassic, U.S.A.). A, B: Part; A: left-lateral view (UV fluorescence); B: line drawing. C, D: counter-part; C: right-lateral view (composite; transmission filters: 400, 500, 600, 650 nm; emission filter: 650 nm); D: line drawing. Abbreviations: dlc, dorso-lateral carina; dm, dorsal midline; ls, left side; pm, posterior margin; rs, right side; tri, transversal ridges; vm, ventral margin. Scales: 5 mm. Photographs: A, Philippe Loubry; C, Christopher Smith. Line drawings: Thomas Laville.

Remarks. There has been a lot of confusion between *Paraostenia* and *Ostenocaris*. *Ostenocaris* was erected for the Sinemurian species, *Ostenocaris cypriformis* (Arduini, Pinna & Teruzzi, 1980), from Osteno, Italy. *Ostenocaris* representatives can be distinguished by particular features such as a sinuous anterior margin, directed antero-dorsally and robust appendages with small spines. *Paraostenia*, which was erected for *Paraostenia voultensis* Secrétan, 1985 from the Callovian La Voulte-sur-Rhône Lagerstätte, France, is actually quite different: its anterior margin is formed of a concave optic notch, its dorsal midline bears a dorsal carina, its posterior margin consists of small concavity. *Paraostenia* representatives are also smaller than those of *Ostenocaris*. The confusion between both taxa comes from figures from Arduini *et al.* (1980; pl. 12, fig. 1; pl. 13). In those figures, specimens assigned to *Ostenocaris cypriformis* have a quite different morphology from *Ostenocaris* and are more likely to belong to *Paraostenia*. In Pinna *et al.* (1985; fig. 6), they actually noticed the particular nature of those specimens, describing them as a “smaller, undescribed species of Thylacocephala showing a well-developed branchial system”.

Based on those differences, some taxa attributed to *Ostenocaris* should then be ascribed to *Paraostenia*: *Paraostenia ambatolokobensis* (Arduini,

1990) nov. comb. from the Dienerian/Smithian of Madagascar and the two specimens originally identified as *Ostenocaris* sp. by Ehiro *et al.* (2015; fig. 10) from the Spathian of Japan. *Ostenocaris* sp. nov. from the Carboniferous of Kansas, mentioned by Briggs & Rolfe (1983: text-fig. 6f) could also fit in *Paraostenia* but it might actually be more related to *Dollocaris* (Middle Jurassic of France, Upper Jurassic of Germany) or *Paradollocaris* Charbonnier in Charbonnier *et al.*, 2017 (Upper Cretaceous of Lebanon). It has a well-developed optic notch with a short rounded rostrum, an antero-ventral corner drawn out as a rounded spine, a convex ventral margin and a posterior margin formed by a notch.

Paraostenia ambatolokobensis (Arduini, 1990)

nov. comb.

Figs 12–13

- 1990 *Ostenocaris ambatolokobensis* Arduini, p. 202, fig. 4
- 1999 *Ostenocaris ambatolokobensis* – Steeman, p. 25
- 2014 *Ostenocaris ambatolokobensis* – Hegna *et al.*, p. 610
- 2014 *Ostenocaris ambatolokobensis* – Schram, p. 354
- 2017 *Ostenocaris ambatolokobensis* – Ehiro *et al.*, p. 279–280
- 2019 *Ostenocaris ambatolokobensis* – Charbonnier *et al.*, tab. 1
- 2019 *Ostenocaris ambatolokobensis* – Ehiro *et al.*, p. 330

Type material. Holotype MSNM i11037.

Type locality. Ambatolokobè, Ankitokazo Basin, Madagascar.

Type level. Middle Sakamena Formation, Dienerian/Smithian, Early Triassic.

Additional examined material. MSNM i19509; MNHN.FA72326. All additional specimens are from the Middle Sakamena Formation, Ambatolokobè, Ankitokazo Basin, Madagascar (Dienerian/Smithian, Early Triassic).

Emended description. Thylacocephala with a folded shield. Antero-posterior axis is the longest (Tab. 1). Soft-parts (eyes, gills, digestive tract, cephalic, raptorial and trunk appendages) are not preserved.

Shield outline. Shield is trapezoidal in lateral view (Figs 12A–D, 13A–D). The anterior margin is formed of a well-developed concave and symmetric optic notch (on). Rostrum is absent. Antero-dorsal corner is abrupt. The anterior part of the dorsal midline (dm) is slightly ascending. The posterior is descending postero-ventrally. The edge between those two parts forms a carina. Postero-dorsal corner is not clearly distinguishable. The posterior margin is narrow (pm) and inclined antero-ventrally. Postero-ventral corner is sharp. The ventral margin is divided into two parts (vm). The posterior half is steeply descending antero-ventrally while the anterior half is horizontal. The antero-ventral corner is rounded. Anterior, posterior and ventral margins are thicker than the rest of the shield, forming a marginal fold (Figs 12, 13A–D).

Shield ornamentation. Long, thin and sinuous ridges running from the optic to the posterior notch cover the entire shield (Figs 12, 13A–F). Between these ridges, short and thin furrows are inserted. Below the dorsal carina, transversal ridges are also present (Figs 12A, B, G, 13A, G). They are formed of coma-like ridges between which thin parallel ridges are inserted. Some coma-like ridges seem to rapidly become longitudinal.

Two longitudinal carinae are visible. A ventro-lateral carina (vlc), parallel to the ventral margin delimits the marginal fold (Figs 12A–E, 13A–D). A dorso-lateral carina runs along almost the entire length (Fig. 13A–D). An anterior transversal groove is parallel to the optic notch, delimiting the marginal fold (Figs 12A–F, 13A–D). No pores nor punctuations are distinguished. The anterior part of the dorsal midline exhibits a row of small tubercles (Fig. 13G).

Cephalic appendages. Two rectangular structures, possibly the *antennula* (atl?) and the *antenna* (ant?), are protruding from the dorsal part of the optic notch (Fig. 13C–E). The dorsal one (i.e., the antennula) ap-

pears thinner and shorter than the ventral one (i.e., the antenna). Segmentation is not distinguishable.

Remarks. The present review of the specimens originally described as *Ostenocaris ambatolokobensis* has indicated that the large, concave optic notch, the abrupt antero-ventral and antero-dorsal corners, the convex dorsal midline with a dorsal carina and the short, slightly concave posterior margin are diagnostic characters of *Paraostenia* and thus we propose the new combination *Paraostenia ambatolokobensis* nov. comb. *Paraostenia ambatolokobensis* differs from *Paraostenia voutlensis* by its more concave anterior margin, its anterior transversal groove and the absence of band of pores in the dorsal area of the shield.

Thylacocephala indet.

Fig. 14

Material. UBGD 30613 (part and counter-part).

Locality. Paris Canyon, west of the Paris city, Idaho, U.S.A. (Brayard et al. 2017).

Level. Early Spathian, late Olenekian, Early Triassic.

Description. Thylacocephala with a folded shield. Antero-posterior axis seems the longest. No trace of soft-parts.

Shield outline. Shield is incomplete in both specimens. Anterior margin is not clearly demarcated, with no clear optic notch. Antero-dorsal corner is drawn out as a sharp, triangular, short rostrum (r; Fig. 14). The rostrum is oriented anteriorly. The dorsal midline is convex (dm). The postero-dorsal corner is rounded. The posterior margin seems short, inclined antero-ventrally (pm). The ventral margin is not well-preserved (vm).

Shield ornamentation. A convex longitudinal carina is visible in the dorsal area of the shield (dlc; Fig. 14A, B). The shield is also formed of transversal ridges oriented antero-ventrally (tri; Fig. 14).

Remarks. Charbonnier et al. (2019; fig. 2e–g) first assigned UBGD 30613 to *Ankitokazocaris triassica*. We actually noticed that it has a separate morphology. First the posterior margin seems oriented antero-ventrally while it is vertical in *A. triassica*. Secondly, it bears transversal ridges oriented antero-ventrally while they are directed postero-ventrally in *A. triassica*. Ridges are common in Thylacocephala (Broda et al. 2020), but they are usually vertical or postero-dorsally oriented. Only three other taxa have such ridges: *Concavicularis elytroides* (Meek 1872) from the Upper Devonian-Mississippian of U.S.A.,

Keellicaris deborae Terruzi & Charbonnier in Charbonnier et al., 2017 from the Upper Cretaceous of Lebanon and *Concavicularis rostellata* from the Pennsylvanian of U.S.A., which has never been formally described (Rolfe 1969: R317, fig. 1401b). *Concavicularis elytroides* has a shorter rostrum compared to the new morphology but the posterior margin looks similar. *Concavicularis rostellata* has a rostrum similar to those specimens but the ridges are oriented posteriorly in the dorsal area of the shield. *Keellicaris deborae* has a very particular morphology: wide posterior and optic notches, large muscle scar and no real rostrum.

UBGD 30613 might also represent a dimorphism among *A. triassica*. With the exception of the transversal ridges, its morphology is quite similar to this taxon. Determining the sex of thylacocephalans is not possible so far (Charbonnier et al. 2017), as there is no knowledge on their reproductive system. The incomplete specimens make difficult any sex determination and then interpretation as a particular taxon. Thus, we decide to keep this taxon in open nomenclature until further discoveries.

DISCUSSION

Preservation

Soft-parts. Soft-part preservation is quite rare among Triassic representatives of Thylacocephala. It was so far only known from China (Ji et al. 2017) and Italy (Arduini 1992; Arduini & Brasca 1984). In Malagasy thylacocephalans only three soft-structures are preserved: compound eyes, antenniform structures and raptorial appendages.

The ultrastructure of the eyes is here described for the first time in *Ankitokazocaris acutirostris*, where hexagonal ommatidia are clearly visible (Fig. 5C, D, F). Preservation of the ultrastructure of the eyes is quite rare in representatives of Thylacocephala. Vannier et al. (2016) made an extensive study of the eyes of *Dollocaris ingens*. They reconstructed the three-dimensional structure of the eyes, including the structure of ommatidia. Each eye had about 18,000 lenses. Ji et al. (2017) also described dense and hexagonal or rhombic ommatidia in one specimen of *Ankitokazocaris chaobuensis* (NIGP 163044; fig. 5a–d). Ommatidia are also preserved in *Ostenocaris cypriformis* (Pinna et al. 1985: fig. 3) from the Lower Jurassic of Italy and in *Concavicularis submarinus* Jobbins et al., 2020 from the Upper Devonian of

Morocco. Compound eyes of *Concavicularis submarinus* are smaller than those of *D. ingens*. They are composed of a dense and relatively regular pattern of hexagonal facets, the latter being convex. Ommatidia of *A. acutirostris* appear larger than those of other representatives of Thylacocephala (*A. chaobuensis*: $w = 100 \mu\text{m}$; *D. ingens*: $w = 40 \mu\text{m}$) but the density of ommatidia is much lower than in *D. ingens* (500 ommatidia per mm^2).

Antenniform structures are protruding from the anterior margin of two specimens of *A. acutirostris* (MSNM i10836: Fig. 5A, B; MSNM i11046: Fig. 6A–D) and one specimen of *Paraostenia ambatolokobensis* (MSNM i19509: Fig. 13C–E). Similar structures have only been mentioned in two other thylacocephalan taxa so far: *Thylacares brandonensis* from the Silurian of Wisconsin and *Mayrocaris bucculata* from the Upper Jurassic of Germany (Haug et al. 2014). Those structures protrude from the optic notch and are often located beneath the eyes. However, it is difficult to assess if they are homologues to antenna or antennula of Eucrustacea as we do not have any information on the segmental origin.

Finally, possible raptorial appendages are preserved in *A. acutirostris*. The raptorial appendages are only distinguishable based on a small rectangular structure protruding from the ventral margin.

Butterfly position. Most Malagasy specimens are preserved in lateral view with the exception of five specimens of *A. acutirostris* preserved in a butterfly configuration. In such specimens, we can clearly see that their shield is not formed of two valves as there is no hinge line (Fig. 7). Betts et al. (2016: p. 479) defined a hinge line as “a moveable articulation point where separate objects are joined or attached”. The thylacocephalan shield is actually folded at the midline, giving the aspect of a “bivalved” shield. We should then advocate the use of folded shield and of left and right sides when describing the shield of thylacocephalans. Use of dorsal midline should also be preferred to the use of dorsal margin.

Butterfly configurations of the head shield is not uncommon in the fossil record of various Euarthropods. For lobsters, the butterfly-like position is characteristic of a moult (Charbonnier et al. 2012; Devillez et al. 2016). This position is also common for “bivalved arthropods” such as bradoriids (Betts et al. 2016; Zhang & Hou 2007), myodocops (Perrier 2011; Siveter et al. 1991), ostracods (Forel et al. 2020; Salas et al. 2007), *Isocyx* or *Tuzoia* (García-Bel-

lido et al. 2009; Vannier et al. 2007). García-Bellido et al. (2009) showed that specimens of *Isoxys* and *Tuzoia* in the butterfly configuration almost never preserve soft parts while those in lateral compression usually conserved soft tissues. They concluded that “butterflied” specimens are probable empty exuviae.

For bradoriids (Betts et al. 2016), *Isoxys* or *Tuzoia* (García-Bellido et al. 2009), besides exuviae, butterfly preservation might be due to post-mortem decay, which would be consistent with the presence of soft-parts in these “butterflied” specimens. During the decay, muscles used for the attachment and the closing of the shield might decompose fast, allowing the shield to take a butterfly configuration. Post-mortem processes may have affected one “butterflied” specimen of *Ankitokazocaris acutirostris* (MNHN.F.A72327: Fig. 7A, B). Indeed, this specimen is preserved with soft-parts (eyes) and might therefore represents a decayed carcass. This hypothesis is made plausible by the potential muscle scar found on the ventral area of the shield of multiple thylacocephalan species (e.g., Charbonnier et al. 2017; Ehiro et al. 2015, 2019; Hegna et al. 2014; Polz 1994).

From the Paris Biota, all specimens are preserved in lateral view but only one specimen of *Ankitokazocaris triassica* and one of *Ligulacaris parisi* preserved trunk appendages. *A. triassica* possessed rectangular elongated structures (pleurites) similar to those described in Devonian and Jurassic representatives (Briggs & Rolfe, 1983; Secrétan 1985).

Ornamentation

Paraostenia ambatolokobensis exhibits an ornamentation unknown in all other representatives of Thylacocephala: the presence of longitudinal narrow ridges with short intercalated furrows on the shield (Figs 12, 13) in addition to coma-like ridges below the dorsal carina (Figs 12G, 13F). Broda et al. (2020) made an important study on the micro-ornamentation of Thylacocephala. They described various kinds of micro-ornamentation: scale, polygons, ridges, pores or setal lumina. However, they never described such ornamentation.

Feeding habits

From Stewart Canyon, one shield of *Ankitokazocaris triassica* is preserved with a posterior pro-

cess of a S0 element of a conodont pertaining to Gondolellidae (N. Goudeband, pers. comm. 2020). The denticles of the element are preserved.

A similar association has already been reported in the Spathian of China by Ji et al. (2017). They reported conodont elements in and on various thylacocephalan shields and also inside potential thylacocephalan coprolites. Following Rolfe (1985), Polz (1990) and Vannier et al. (2016), Ji et al. (2017) proposed a visual predatory lifestyle for *Ankitokazocaris chaobuensis* feeding on conodont animals. Using their hypertrophied compound eyes, thylacocephalans would have been able to detect their presence and catch them with their raptorial appendages. Jobbins et al. (2020) also suggested that preys of thylacocephalans were smaller animals such as conodont animals.

However, based on the studied Stewart Canyon specimen, it appears rather difficult to confirm such relationship hypothesis between conodont animals and Thylacocephala. Indeed, this unexpected presence of a conodont element might be either a residue of digestion or only a preservation artefact, both organisms being superimposed.

Different preys were also proposed: Pinna et al. (1995) reported vertebrae of Teleostei and Selachimorpha, hooks of Cephalopoda and shells of other eucrustaceans and thylacocephalans in the stomach contents of *Ostenocaris cypriformis*. Vannier et al. (2016) also reported eucrustacean fragments inside the stomach of *Dollocaris ingens*. All of these findings suggest a predatory or necrophagous lifestyle for Thylacocephala.

Diversity and distribution of Early Triassic Thylacocephala

Thylacocephalans are assumed to have been the most diversified during the Triassic. (Ehiro et al. 2019). However, our results show that the taxonomic diversity of Triassic Thylacocephala has been slightly over-estimated, with an actual reduced number of revised species (17 before, 15 now). This value is almost similar to the number of species described in the Devonian (14; Briggs & Rolfe 1983; Broda et al. 2020; Chlupáč 1963; Jobbins et al. 2020). Nevertheless, the Triassic is certainly the richest period in terms of thylacocephalan-bearing outcrops: 19 localities are now known from nine different countries (Australia: Haig et al. 2015; Austria: Forchielli & Pervesler 2013; Glaessner 1931; China: Feldmann

et al. 2015; Ji et al. 2017; Yan-bin 1983; Italy: Affer & Teruzzi, 1999; Arduini 1988, 1992; Arduini & Brasca 1984; Dalla Vecchia 1993; Dalla Vecchia & Muscio 1990; Pinna 1974, 1976; Teruzzi & Muscio 2019; Japan: Ehiro et al. 2015, 2019; Madagascar: Arduini 1990; Slovenia: Križnar & Hitij 2010; Spain: Calzada & Mañé 1993; U.S.A.: Charbonnier et al. 2019, this work). At a smaller timescale, only one taxa is documented from the Smithian while seven are reported from the Spathian (Tab. 1). Nothing is presently known on the consequence of biotic crises on thylacocephalan diversity, probably due to the scarce fossil record of these organisms. For instance, only one potential thylacocephalan species is known in the Permian (*Coreocaris eishunensis* Kobayashi, 1937 from the Lower Permian of South Korea; Vannier et al. 2006) and no occurrences are known in the Early Triassic before the Dienerian. Such a large gap in the fossil record of Thylacocephala is a crucial issue, preventing detailed studies of the macro-evolution of this group. Our knowledge of their evolution thus remains very fragmented.

The scarce fossil record of Thylacocephala might also influenced the known pattern of their palaeogeographic distribution. As noticed by Ehiro et al. (2019), during the Triassic, the distribution of Thylacocephala is constrained so far to low-latitude Tethys and Panthalassa.

CONCLUSION

New observations on Malagasy representatives of Thylacocephala provide important information on the morphology and on the anatomy of these organisms. *Ankitokazocaris acutirostris* and *Paraostenia ambatolokobensis* are only the third and fourth thylacocephalan taxa for which possible cephalic appendages are reported. The discovery of additional specimens bearing such structures is a prerequisite to precisely characterise them. In addition, an unexpected new type of micro-ornamentation is reported for *Paraostenia ambatolokobensis*.

New thylacocephalan occurrences in the Paris Biota are reported, with the description of a new morphology and the reassignment of *Pariscaris triassica* to *Ankitokazocaris triassica* nov. comb. Those new occurrences provide important insight on the taxonomic diversity of Thylacocephala in the Early Triassic and led to the revision of Early Triassic

taxa from Japan and China. The Triassic was considered as the period showing the highest species richness of Thylacocephala although it does not represent the highest level of morphological diversity. In light of this study, the taxonomic diversity of Early Triassic thylacocephalans was slightly over-estimated. Overall, the Triassic is likely the richest period in terms of thylacocephalan-bearing outcrops, but probably not in terms of taxonomic diversity.

Supplementary material.

Measurements on Malagasy and Idaho Thylacocephala and script for descriptive statistics:

<https://doi.org/10.5281/zenodo.4066340>.

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