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The end of the 'living fossil' tale? A new look at Triassic specimens assigned to the tadpole shrimp *Triops cancriformis* (Notostraca) and associated phyllopods from the Vosges region (eastern France)

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Abstract: Notostracan branchiopods reported from the Lower Triassic Voltzia Sandstone Lagerstätte in northeastern France have previously been assigned to *Triops cancriformis*, making this species the longest persisting animal in earth history. Careful restudy of the splendidly preserved material indicates that the species can be well characterized but represents a notostracan genus and species that cannot be assigned to the Triopsidae. This undermines the concept of its being a 'living fossil'. The name *Apudites antiquus*, under which the first known specimens were described, is available and appropriate for the species. Some of the specimens of *Apudites antiquus* offer morphological details of a quality that ranks them among the best-preserved fossil non-marine arthropods. The Voltzia Sandstone specimens previously assigned to the extant species *T. cancriformis* include two additional, peculiar diplostracan branchiopods, *Olesenocaris galli* gen. et sp. nov. and *Grauvogelocaris alsatica* gen. et sp. nov., both with unique morphological features that characterize them as representatives of as yet unknown families.

Key words: Notostraca, Diplostraca, Branchiopoda, Triassic, Central European Basin, living fossil.

THE term 'living fossil' is used for species or genera that exist with a more or less unaltered morphology over geologically long periods until today. Although the term has no practical meaning with regard to evolutionary processes and mechanisms, it has been regularly used in biological and palaeontological textbooks over the last century as if it conveys a particular meaning. The term was coined by Charles Darwin and is used in the first edition of his *Origin of the Species* (Darwin 1859), which may have contributed to its general acceptance and its eminent attention. However, Darwin applied the term to the Australian duck-billed platypus and to the South American lungfish, neither of which were known from fossils at the time. In fact, since Darwin the phrase 'living fossil' has been used in at least six different ways (Schopf 1984). Typical living fossils of modern textbooks include *Gingko*, *Latimeria*, *Limulus*, *Lingula*, *Nautilus* or *Sphenodon*, all of which are in a strict sense known only from Recent species, but appear(ed) to have close relatives in the fossil record, which date back into pre-Cenozoic periods of the Earth history. Among the crustaceans, the decapod family Glypheidae merits mention. It was originally known from fossil material, but two extant species were subsequently discovered near the Philippines (Forest *et al.* 1976; Forest 2006).

To some, the only true 'living fossil' that would indeed merit its designation is the branchiopod species *Triops cancriformis* (Bosc, 1801), which in addition to the living specimens was also claimed to be identified from Late Triassic strata in Franconia, Germany (e.g. Trusheim 1938; Kelber 1998a) and subsequently from Early Triassic strata of the Vosges region, northeastern France (e.g. Gall 1971) and Late Triassic strata in the Culpeper Basin of Virginia, USA (Gore 1986). According to the generally accepted narrative a few decades ago, it represents a species that has survived for 240 myr with an unaltered morphology. The species received so much general attention for its apparent longevity that it became an exceedingly popular item for aquarists, known as 'aquasaurs', 'prehistoric tadpole shrimp' or (in German) *Urzeitkrebse*. Ironically, this even turned the story of *Triops cancriformis* upside down, when the British newspaper *The Guardian* announced the 'World's most ancient creatures found in Scottish field' and reported that colonies of 'the world's oldest living

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creatures . . . have been found alive' (*The Guardian*, 29 July 2010).

Since then, doubts have arisen about the specific identity of the triopsid fossils and they have been discussed in varying contexts (e.g. Mantovani *et al.* 2004, 2008; Lucchetti *et al.* 2006; Garrouste *et al.* 2009; Vanschoenwinkel *et al.* 2012; Atashbar *et al.* 2013; Mathers *et al.* 2013a; Horn & Cowley 2014; Kin & Błażejowski 2014; Wagner *et al.* 2017; Lidgard & Love 2018). Many of these publications (i.e. Vanschoenwinkel *et al.* 2012) provide molecular studies that challenge even a pre-Cenozoic origin of modern notostracans such that *Triops cancriformis* could not be claimed to have existed during the Mesozoic. However, all of these publications are hampered by the fact that the available fossil material from the Late Triassic of Franconia, southern Germany, and particularly the equally identified specimens from the upper Buntsandstein Voltzia Sandstone Formation of the Vosges region, eastern France, has not been examined in sufficient detail to clarify its precise morphological characters despite a number of commendable studies (Trusheim 1938; Gall 1971; Kelber 1998a, 1999; Wagner *et al.* 2017, 2019). To overcome this deficiency, the original material of Louis Grauvogel from the Voltzia Sandstone Formation ('Grès à Voltzia') was studied in detail for the first time for this study. A plethora of specimens from the Keuper beds of Franconia have been re-examined and will be described separately.

HISTORY OF DISCOVERY

Fossils assigned to the genus *Triops* were initially known from the upper Carboniferous (Guthörl 1934) and from the uppermost Buntsandstein (initially described as *Apudites antiquus* Schimper, 1853). However, the discovery of exquisitely preserved notostracan branchiopods in the Carnian Keuper beds of the Steigerwald region in Franconia, southern Germany, by Trusheim in 1934 was fairly unexpected (Trusheim 1938). The significance of the Franconian specimens seems to have been recognized immediately. Trusheim studied the material in detail and wrote a methodical study, in which he identified the specimens as representing a new subspecies, *Triops cancriformis minor*, of the common Recent species *T. cancriformis*.

Nevertheless, a reevaluation of Trusheim's data and material from the Voltzia Sandstone Formation ('Grès à Voltzia', upper Buntsandstein) of the Vosges region, northeastern France (Gall 1971; Gall & Grauvogel-Stamm 2005) suggested that the Franconian material represented the same species (or subspecies) as that from the Voltzia Sandstone. Consequently, most authors dealing with Triassic faunas believed that the Triassic European notostracan fossils were conspecific with the common recent notostracan, *Triops cancriformis* (e.g. Dechaseaux 1953; Longhurst 1955a, 1955b; Kelber 1998a, 1998b, 1999; Mantovani *et al.* 2004; Kelber & Nitsch 2005; Zierold *et al.* 2007; Gómez & Zierold 2008; Voigt *et al.* 2008).

Eventually, it came as a second surprise that numerous additional specimens of *Triops* occur in strata of the Hassberge region in Franconia, just *c.* 20–30 km north of Trusheim's locality in the Steigerwald region. The discovery of these specimens was subsequently supplemented by numerous additional specimens from strata in nearby localities in the Hassberge Formation. Preliminary descriptions of this new material (Kelber 1998a, 1998b, 1999; Kelber & Nitsch 2005) complemented Trusheim's description and provided data for a modern analysis such that the new material was described as *Triops cancriformis* as well.

An additional taxonomic complication arose from the findings of material described as an additional subspecies of *Triops cancriformis*, *T. c. permiensis*, from Permian playa strata in the Lodève basin, southern France (Gand *et al.* 1997). Furthermore, numerous carapaces and trunk fragments have been collected from the Upper Triassic (Rhaetian) Bull Run Formation in the Culpeper Basin in Virginia, USA (Gore 1986). The specimens from Virginia possess a rudimentary supra-anal plate (Gore 1986, fig. 3.1), which is not developed in *Triops*. Nevertheless, the specimens were identified as *Triops* cf. *cancriformis*.

A modification in phylogenetic ideology led to a change in the paradigmatic view of living fossils in general and the identity of the fossil material of *Triops cancriformis* in particular during the last two decades: a simplistic view based on superficial similarities of dorsal shield outlines and proportions, as well as abdominal and telson shapes that dominated the identifications until the 1980s, shifted towards partly hypercritical views of morphological characters of fossil specimens, triggered also by the application of molecular DNA analyses for phylogenetic reconstructions and age estimations (e.g. Murugan *et al.* 2002; Mantovani *et al.* 2004, 2008; Korn *et al.* 2006, 2013; Lucchetti *et al.* 2006, 2019; Hegna & Ren 2010; Hegna 2012; Mathers *et al.* 2013a, 2013b, 2015; Horn & Cowley 2014; Wagner *et al.* 2017, 2019; Lidgard & Love 2018). Neither of these studies does consider further complications resulting from aspects such as cryptic or pseudocryptic species, which appear to be particularly sensible in the field of crustacean taxonomy (e.g. Lajus *et al.* 2015).

Most of these discussions on the living fossil status of *Triops cancriformis* are conceptual and far removed from a critical examination of the Franconian and Vosges material. A study on Devonian tadpole shrimp (Lagebro *et al.* 2015) tacitly raised the Triassic material to species level, *T. minor* in their figure 7, raising Trusheim's subspecies designation to that of species. A close examination of material from the Hassberge region (Wagner *et al.* 2017) reveals gaps in the description. Wagner *et al.* (2017) rejected a *T. cancriformis* identity for the Hassberge material on the basis of the shape of the dorsal carapace and its change during ontogeny. This led to a taxonomically awkward assignment of the material as 'Notostraca *minor*'; a strategy meant to avoid a traditional genus-level assignment, and instead apply the next higher reliable node in its place. To date, no publication has examined whether or not the Steigerwald, the Hassberge and the Vosges localities did indeed preserve the same species of *Triops*.

GEOLOGICAL SETTING OF THE SUPPOSED *TRIOPS*-BEARING STRATA OF THE VOLTZIA SANDSTONE

The Voltzia Sandstone Formation ('Grès à Voltzia') forms the upper part of the upper Buntsandstein (lower Anisian) in the Vosges region. The lower part of this formation is dominated by a sandstone member termed the 'Grès à meules', which has a thickness of 10–12 m in the northern Vosges region and contains amazingly diverse faunal assemblages of plants (including the eponymous conifer *Voltzia*), invertebrates, vertebrates and ichnofossils (e.g. Schimper 1853; Bill 1914; Grauvogel 1947a, 1947b, 1947c, 1947d, 1951a, 1951b, 1951c; Grauvogel & Laurentiaux 1952; Grauvogel & Gall 1962; Grauvogel *et al.* 1967; Gall 1971; Grauvogel-Stamm 1978; Gall & Grauvogel-Stamm 1993, 2005). The superb quality and enormous diversity make the fossil-bearing Voltzia Sandstone horizon one of the most important Triassic fossil Lagerstätten.

This sandstone member is typically composed of lenticular bodies of generally grey to pink, fine-grained feldspathic sandstone that are amalgamated in thick sandstone units. However, the sandstone facies changes swiftly locally both laterally and vertically and includes clayey to silty and dolomitic interbeds. It records coastal fluvial to deltaic depositional environments. Silty to clayey rocks in the succession have been formed in brackish water ponds and small lakes, and they are dominated by biocoenoses with abundant benthic arthropods, including the notostracan specimens, spinicaudatans, ostracods, syncarids, isopods and other crustaceans, but also include numerous other invertebrates (see references cited above).

LOCALITIES, MATERIAL & METHOD

The extraordinarily preserved fossils of the shale lenses of the Grès à meules member of the Voltzia Sandstone were collected during decades of careful examination of the rocks by Louis Grauvogel (partly in cooperation with Jean-Claude Gall during the latter part of the activities). The notostracan material was collected by Louis Grauvogel in three quarries: the Bopp-Dintzner quarry near Arzviller (east of Sarrebourg; N 48°43′40″, E 7°11′05″); the Philippe quarry near Vilsberg (WNW of Saverne; N 48°46′55″, E 7°14′45″); and the 'carrière royale' quarry ('Königsgrube') near Soultz-les-Bains (Sulzbad, west of Strasbourg; N 48°34′35″, E 7°29′30″) (Fig. 1). In total, 22 specimens have been recorded by Gall (1971, p. 38), which agrees with the manifest of material transferred to, and now housed in, the collection of the Staatliches Museum für Naturkunde, Stuttgart (SMNS; except for one specimen missing from the original Grauvogel collection, Ap1, Gall 1971, pl. 7.3). A century earlier, Schimper collected notostracans from one of the three quarries that delivered Grauvogel's material and described them as belonging to a new genus and species *Apudites antiquus* (Schimper 1840, 1853). Unfortunately, his material was never adequately figured and is now lost.

Grauvogel's specimens are not accurately labelled and generally lack information on the locality from which they were collected. Many of the Grès a Voltzia specimens were coated with some sort of varnish to prevent degradation of the remains and to help maintain the integrity of fissile shale. Unfortunately, such a coating inhibits modern studies of preservation using scanning electron microscopy and energy-dispersive x-ray spectroscopy. In addition, photography with documentation of fine details that are preserved in several specimens (although fewer than half of the available ones) posed problems. They were overcome by various techniques but required in some cases sophisticated photoshopping that led to a minor decrease in the quality of the final images.

Nonetheless, the lithology of the samples clearly indicates differences that strongly suggest different origins. The vast majority conforms to the lithology of the two specimens figured in Gall (1971), which are known to originate from near Vilsberg. The quarry near Soultz-les-Bains is the classical 19th century locality, from where Schimper's material was collected, including several specimens described as *Apudites antiquus* (Schimper 1840, 1853, pl. 3), which were the earliest fossils subsequently attributed to the modern notostracan genus, *Triops*.

The systematic relationships of the three genera and species from the Voltzia Sandstone dealt with herein are shown in a phylogenetic tree. This tree is based on robust cladistic analyses discussed in detail in Hegna (2012).

The nomenclature for the postcephalic anatomy of notostracans requires some clarification in how we apply it to fossil specimens. Modern notostracans have a region of 11 limbs that correspond one-to-one to body segments behind the head; this region is called the thorax. Behind

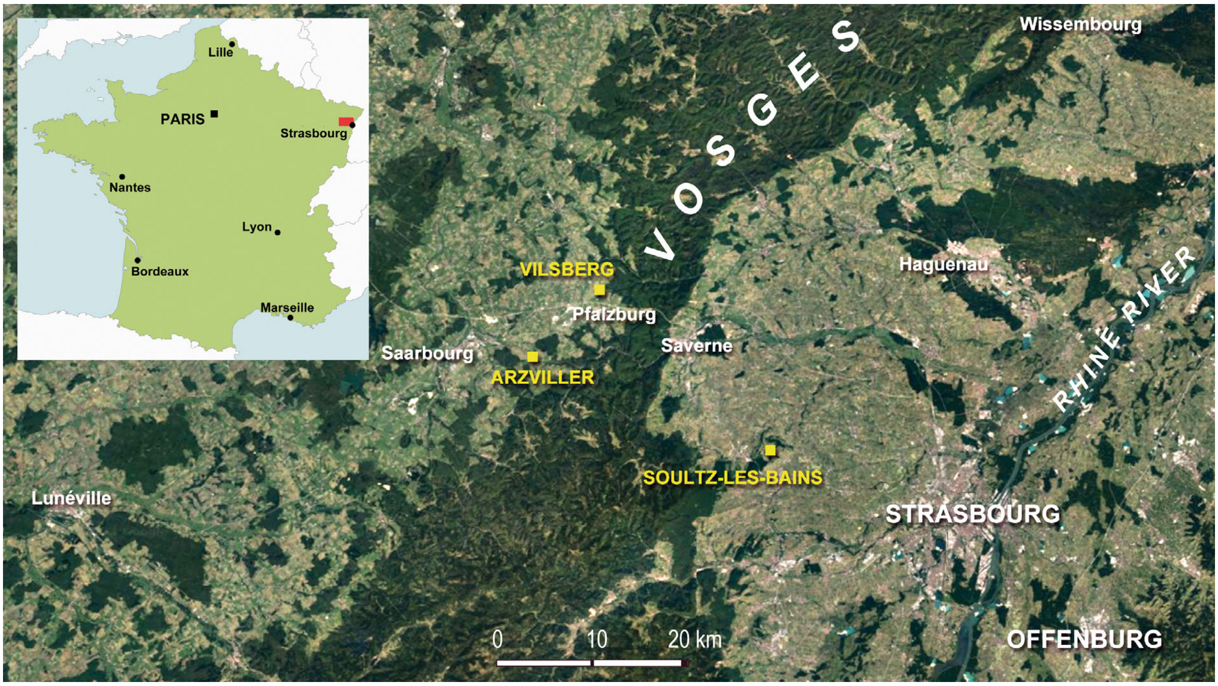


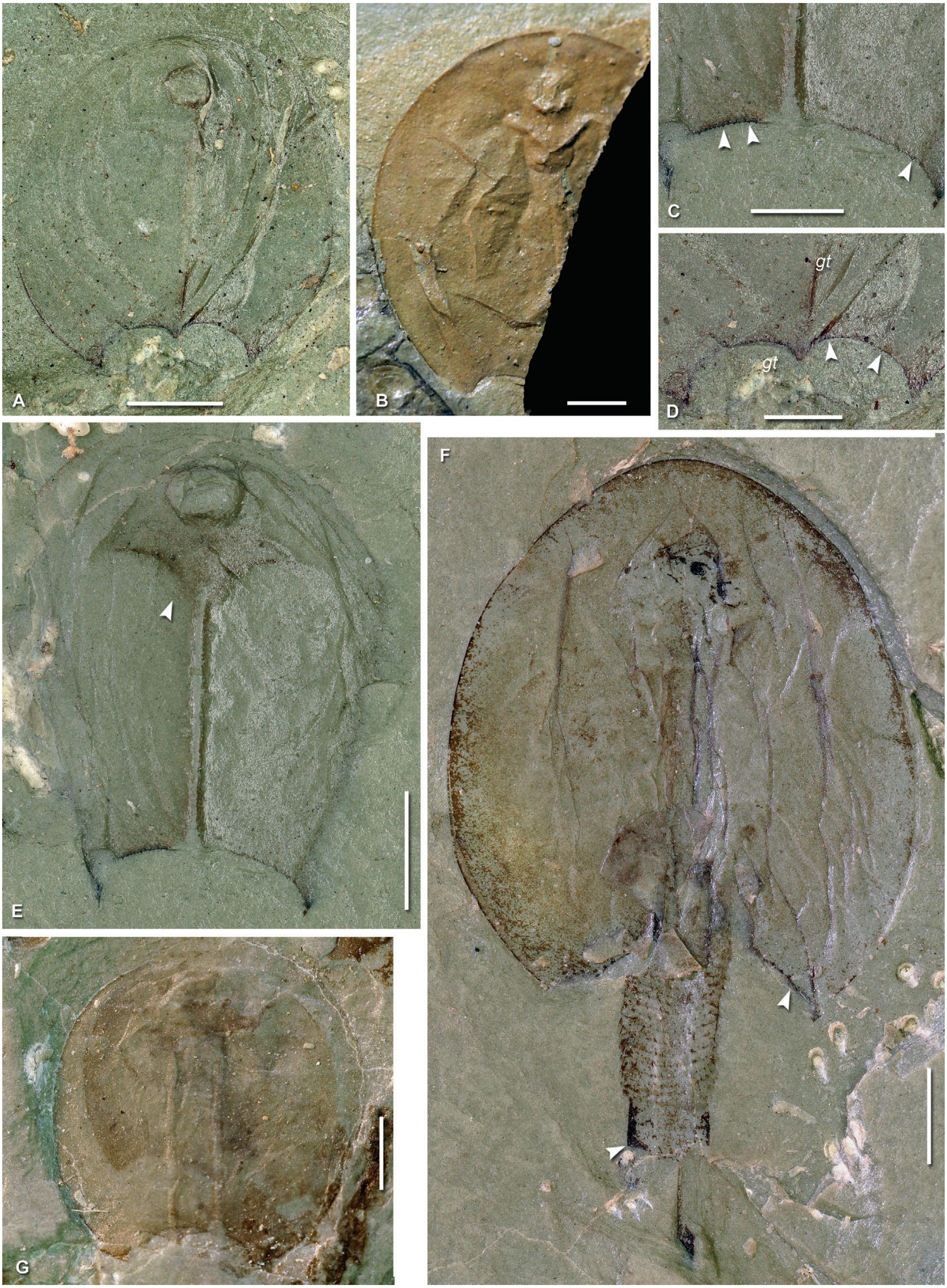
FIG. 1. Map of France and satellite photo of the Alsace region, northern France, with the location of Louis Grauvogel's collecting localities of notostracans from the Voltzia Sandstone Formation. Red rectangle on insert indicates the location of the satellite map. Map data: Google, Landsat/Copernicus, GeoBasis-DE/BKG ©2009.

the eleventh limb, the limbs begin to decrease in size and become increasingly closely spaced until they disappear. In fact, the limbs lose their one-to-one correspondence with the dorsal segmentation (which remains regular and uniform). The entire region (from eleventh limb to telson) is referred to as the abdomen. No term exists to differentiate the limb-bearing and the limbless regions of the abdomen. Identifying the thoracic–abdominal division in fossils is difficult. The overlapping nature of the appendages (both thoracic and abdominal) make identification of the precise number difficult. Prior usage of the terms for fossil specimens often requires an assumption that the boundary was at the eleventh segment in the past as well. We have attempted to use this terminology, but must point out its shortcomings in advance.

PRESERVATION & TAPHONOMY

Differences in preservation may greatly affect the morphology seen in fossil calmanostracans. Nevertheless, such differences may also contribute to a better understanding of the fossil remains. Freshly moulted notostracan exoskeletons, if they have not experienced significant turbulence, will retain the fine appendages; the completeness giving the superficial appearance of a carcass.

FIG. 2. *Apudites antiquus* Schimper, 1853. A, D, SMNS 75644-8a, small, dorsoventrally compressed carapace; note subcircular eye tubercle with faint posterior indentation and end of carina creating a bilobate course of the notch: A, entire specimen; D, magnification of the posterior part with minute spines along margin of recess (arrows). B, SMNS 75644-2a, partial dorsoventrally compressed carapace with wrinkles and small cracks resulting from compaction; eye tubercle with small posterior indentation and cervical groove well recognizable. C, E, SMNS 75644-9a: C, magnified posterior margin of small carapace exhibiting minute spines along margin of recess (arrows); E, dorsal view of the external cast of the dorsoventrally compressed small carapace with spines along margin of posterior indentation and well-developed carina, subcircular eye tubercle with slight posterior indentation, and vestiges of the ventrally located labrum and attachment site of the soft parts (posterior margin marked by arrow). F, SMNS 75644-18b, nearly complete specimen preserved in a flattened 3D manner with longitudinal cracks of the carapace resulting from dorsoventral compaction, ventral view; margin of notch with small spines and sharp thorn-like posterolateral corner of telson arrowed. G, SMNS 75644-13a, nearly complete carapace preserved in a flattened 3D manner with detached and shifted ventral tissue (responsible for doublure of carina and posterolateral spine next to centre of recess) and overlying at least one additional specimen visible as a blurry darker area. Scale bars represent: 1 mm (A, E–G); 2 mm (B); 500 μm (C, D).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However, such moulted remains will lack the original three-dimensionality of a carcass, and furthermore, ecdysis often separates the carapace from the rest of the dorsal exoskeleton. Conversely, if a carcass is allowed to decay for several days, the less-resistant internal tissues will decay first; taking with them the original convexities of the remains. Thus, a decayed carcass can come to resemble a moulted exoskeleton (e.g. Hegna 2012, fig. 20.4–5). However, a moulted exoskeleton will (under normal circumstances) never possess an infilled gut, whereas a carcass may have lost the internal tissues due to decay while still retaining the gut filling. Complete specimens having undergone little decay, and by contrast are regularly preserved with a notable convexity of the carapace (e.g. Gand *et al.* 1997; but see also Waskom *et al.* 2023). Nevertheless, near-complete specimens collected from the Voltzia Sandstone are mostly flattened individuals, both as dorsoventrally as well as laterally compressed specimens.

The examined specimens from the Voltzia Sandstone differ considerably in their preservation. Some of them are preserved as isolated carapaces (Fig. 2). Others have retained parts or the entire trunk with ventral appendages (e.g. Figs 3–5). Soft-part deformation is a regular feature seen in the examined specimens. This can be recognized in twisted, and laterally as well as anteriorly or posteriorly moved limbs, and also in a shift of the entire set of ventral appendages (e.g. Figs 3A, 4C, 5D) or the alimentary canal in respect to the carapace (Fig. 3A). Some of the studied specimens have a trunk that is somewhat telescoped inward underneath the carapace (e.g. Fig. 3A). A fresh carcass would not be able to contort into such positions, owing to the constraints placed on its movement by the internal muscles; once those muscles have decayed, the exoskeleton is free to assume any manner of position.

Relics of the digestive tract are partly preserved with a dark brown tint, often dispersed as a halo (e.g. Fig. 5D). The mode of formation of such colouration relates to rapid burial of specimens and has been the subject of intensive studies that have provided systematic data on the decay susceptibility of cuticular body parts and soft-tissue organs, and the contribution of bacteria to the processes (e.g. Hegna 2012; Butler *et al.* 2015; Van Houte *et al.* 2022). This type of preservation is now explained as dependent on structural stability obtained from the cuticular lining of the gut, microbial replacement of gut epithelium and gut infilling rather than true soft-tissue preservation (e.g. Lerosey-Aubril *et al.* 2012; Liu *et al.* 2018; Steiner 2018).

Desiccation may have also affected the dorsal exoskeleton in allowing the development of wrinkles by a reduction of the rigidity of the hydraulic body and subsequent slight compression. Nevertheless, the majority of wrinkles on the carapace are more likely to be due to dorsoventral compaction, which not only affected the convexity of the shield but also formed wrinkles to accommodate the transformation of a 3D structure into a 2D structure (similar deformational features being recognized from specimens of the Chengjiang Lagerstätte).

SYSTEMATIC PALAEONTOLOGY

Class BRANCHIOPODA Lamarck, 1801 emend. Latreille (1817)

Remarks. For the revised view of ranking according to the principles and rules of phylogenetic nomenclature see Hegna & Olesen (2020).

Subclass PHYLLOPODA Preuss, 1951

Remarks. As used by authors during the last 15 years (e.g. Richter *et al.* 2007; Olesen 2009), the taxon Phyllopoda encompasses the phylogenetic group that includes tadpole shrimps, clam shrimps and water fleas. Notable morphological criteria, viable in fossils, that support the monophyly of Phyllopoda include internalized compound eyes (i.e. not stalked as in anostracans), telsonal setae, and a dorsal carapace (used in this study as a term for the stiffened protective cover of the cephalothorax). The primitive state of the carapace in the ancestral phyllopod is not clear; it is relatively flat in the lineage leading to notostracans, but folded laterally in diplostracans. It is quite conceivable that the absence of a carapace in anostracans may represent a reduction of the carapace, rather than a ‘naked’ primitive state of the branchiopod clade.

Subclass CALMANOSTRACA Tasch, 1969
Order? NOTOSTRACA Sars, 1867

Remarks. Notostraca, according to recent usage, is seen as a broad concept. Rather than restricting the order to the crown group representatives, it has been used explicitly (Lagebro *et al.* 2015) or implicitly (Werneburg & Schneider 2023) as a ‘total group’; including both crown group representatives (e.g. *Triops* and *Lepidurus*) as well as extinct members of the stem lineage. Doing this runs the risk of making the group paraphyletic, given that the kazacharthrans almost certainly arose from the same stem lineage. This, in essence, is the same situation as outlined by Hegna & Ren (2010). Due to these issues, the use of Notostraca is treated with caution. *Apudites* (discussed below) fits within Notostraca according to Werneburg & Schneider's (2023) usage, but almost certainly lies outside the crown group notostracans.

Genus-level distinctions within the Triopsidae Keilhack, 1909 are trivial on a neontological level, with only the genera *Triops* Schrank, 1803 and *Lepidurus* Leach, 1819 distinguished to date. Both are easily discriminated so that genus-level diagnoses are rarely considered in the literature. Fossil notostracan genera formally described to date include *Strudops* Lagebro *et al.*, 2015 from the Upper Devonian of Belgium; *Lynceites* Goldenberg, 1870 from the upper Carboniferous of the Saar Basin, Germany and also reported from Canada (Copeland 1957); *Heidiops* Werneburg & Schneider, 2023 from the lower Permian of the Lodève Basin, France; *Prolepidurus* Chernyshev, 1940 from the Lower Cretaceous (also claimed sometimes from Jurassic strata) of the Transbaikal (Забайкалья) region in Russia; *Discocephala* Hong, 1985 (the first use of this name is in the eponymous family name: Discocephalidae Hong, 1985; but see discussion below under *Apudites*) and *Dikelocephala* Hong, 1985, both from the Lower Triassic of North China; *Weichangiops* Yang & Hong, 1980 and *Brachygastriops* Yang & Hong, 1980, both from the Upper Jurassic of North China; and *Chenops* Hegna & Ren, 2010 and *Jeholops* Hegna & Ren, 2010, both from the Lower Cretaceous of North China. *Weichangiops* and *Brachygastriops* have been revised and regarded as junior synonyms of *Lepidurus* (Chen 1985; see also Lu 2008). These two genera, as well as *Discocephala*, were subsequently suggested to be synonyms of *Prolepidurus* (Hegna & Ren 2010).

The majority of notostracan crustaceans from the Devonian to the Triassic are characterized by a dorsoventrally flattened, subcircular to longitudinally elongate dorsal shield that covers the cephalon and a considerable part of the trunk. The posterior region of the dorsal shield has a notch that is bounded posterolaterally by angular or slightly pointed corners. The cephalon carries a relatively broad labrum and bulky crescentic mandibles (both the mandibular articulations and muscle attachment sites are visible on the dorsal surface of the carapace). The thorax has a slightly variable number of appendages, but mostly ranging in the order of 10–13 (although often difficult to count with certainty in fossils; only 11 in the thoracic series in extant species). The cylindrical abdomen consists of relatively few to considerably many segments (ranging from 6–14 in *Strudops* and 18–20 in *Heidiops* up to slightly more than 30 in *Apudites antiquus* described below, and up to more than 40 in the specimens assigned to *Triops cancriformis minor* from the Hassberge region), all being well-defined. The telson is relatively small and fairly simple in outline, carrying a paired caudal furca.

These phylogenetically old genera and species certainly do not represent a monophyletic group; instead, they occur at points within the notostracan and calmanostracan stem groups (Hegna, 2012). They are separated from the crown group notostracans (i.e. the members of the family Triopsidae, with the almost exclusively extant genera *Triops* Schrank, 1803 and *Lepidurus* Leach, 1819) by a number of 'primordial' features.

Castracollis Fayers & Trewin, 2003 (type species: *C. wilsonae* Fayers & Trewin, 2003) from the Lower Devonian (Pragian) Rhynie Chert of Aberdeenshire, Scotland, is the oldest known notostracan-like genus. Known specimens are incomplete but are suggested to have had a body plan reminiscent of modern notostracans with a labrum and robust mandibles. The authors also provide a reconstruction with a domed carapace and a biramous second antenna, but these features are not clearly visible in the photographs. The trunk consists of numerous segments composed of similar somites, with a thorax of up to 26 segments. The anterior 11 segments possess long, phyllopodous appendages, the remainder variably possess 10–15 phyllopodous appendages with a disposition of one per somite. The abdomen consists of up to 28 apodous segments (Fayers & Trewin 2003). The telson is apparently very long, with posterolateral spines, which distinguishes the genus and species considerably from all undisputed notostracans. As a result, this genus and species combination is considered to represent its own higher taxon, the order Castrocollida (Schram & Koenemann 2022).

Strudops Lagebro *et al.*, 2015 from the Upper Devonian of Belgium, differs from the extant members of the Triopsidae, as well as from most other notostracans, by the absence of a dorsal carina, the absence of spines at the posterior notch of the carapace, and the relatively broad (transversely), but short and paucisegmented trunk. *Strudops* appears to have limbs developed at the abdomen (although difficult to recognize) and a somewhat more anteriorly attached anteriormost thoracic limb. These characters have previously not been regarded as particularly profound in a phylogenetic context. In addition, the telson has a subrectangular outline with a slight tapering rearward, similar to that seen in the notostracan specimens identified as *Triops cancriformis* from the Voltzia Sandstone Formation (Gall 1971) as well as from the Keuper beds of the Hassberge region, Franconia (Kelber 1998a, 1999), and also in some of the extant species of *Triops*.

Heidiops Werneburg & Schneider, 2023 (type species: *Triops cancriformis permiensis* Gand *et al.*, 1997) from the lower Permian (Kungurian) of the Lodève Basin, France, is primarily characterized by a conspicuous differentiation of thoracic and abdominal segments changing in the course of ontogenetic development; a telson with a thickened, ring-like furcal joint; and flat remnants of compound eyes on the carapace. The carapace has a median dorsal carina and is longitudinally elongated in outline, with pointed posterolateral corners. The trunk is relatively short, but consists of up to 20 segments. The thoracic limbs appear to lack phyllopodous exopods, but this may be a preservational artefact because exopods are much thinner and more weakly sclerotized than the endopods. Werneburg & Schneider (2023) described the posterior trunk as being devoid of abdominal limbs, but the figures in Gand *et al.* (1997, figs 17 and 19.1,4) suggest the presence of limbs. The telson of *Heidiops* is short, and bears pits that are considered as loci for sensory setae (Werneburg & Schneider 2023).

Lynceites Goldenberg, 1870 from the upper Carboniferous of the Saar Basin, western Germany, has a carapace with a median dorsal carina and pointed posterolateral corner, which is variable in outline, but sometimes broader (tr.) than long (sag.). It has a mandibular bulge, a dorsal organ and maxillary glands but does not show compound eyes and maxillary bulges. The trunk is shorter than the carapace and consists of up to 20 segments. As with *Heidiops*, it was regarded as lacking phyllopodous exopods on the thoracic limbs and abdominal limbs (Werneburg & Schneider 2023), but this absence may, more plausibly, be due to decay rather than evolution. The telson is short, flat, and does not show any recognizable morphological structures (Werneburg & Schneider 2023).

Prolepidurus Chernyshev, 1940 (as characterized by its type species, *P. daja*) has a naupliar eye surrounded by a large depression, but this may result from deformation. In any case, the genus and species has a subrectangular to slightly subtrapezoidal telson with a small median anal plate.

The genus *Xinjiangiops* with three species (*X. suni*, *X. keejianensis* and *X. toksunensis*) was introduced by Hong (1980) for specimens from the Middle Triassic Keelamayi Formation of the Turpan Basin, northern Xinjiang, with an additional four species (and two apparently unpublished manuscript names) introduced by Yang & Hong (1986). All species are nearly exclusively known from isolated broad carapaces with broadly curved posterolateral margins leading into a moderately broad indentation that ends in a narrow median sulcus. The eye tubercle is subtriangular, largely formed by laterally extended dorsal organs, which appear to vary in size between the species. Accordingly, the carapace indeed offers characters typical for the Kazacharthra rather than the Notostraca. The only apparently known trunk is described as being composed of 17 segments. The genus and species were revised by Chen & Zhou (1985), who identified them as the kazacharthran *Almatium gusevi* (Chernyshev, 1940); a species originally described from Kazakhstan and revised by Novojilov (1957, 1959). Chen & Zhou (1985) presented more and better-preserved material from the Upper Triassic Huangshanjie Formation, which nicely illustrates the morphology of the trunk and telson. Chen & Zhou's (1985) work was missed by Yang & Hong (1986), and thus, Yang & Hong's (1986) paper is the most recent treatment. A complete synonomy of all kazacharthrans will be presented by Hegna *et al.* (unpub. data 2024).

Weichangiops Yang & Hong, 1980 is based on two species, *W. triangularis* Yang & Hong, 1980 and *W. rotundus* Yang & Hong, 1980, both from the Upper Jurassic of the Hebei Province, North China. Yang & Hong (1980) notably regarded both the family Triopsidae, and their newly created subfamily Weichangiopsinae Yang & Hong, 1980, as possessing one eye. This is a fundamental misunderstanding of notostracan anatomy, and may have been caused by mistaking the dorsal organ for a single eye. As mentioned above, *Weichangiops* and *Brachygastriops* were regarded as junior synonyms of *Lepidurus* (Chen 1985) and subsequently to be synonyms of *Prolepidurus* (Hegna & Ren 2010). *Weichangiops* was returned to current usage by Liao *et al.* (2020, fig. 2C) in a figure caption without a supporting taxonomic justification.

Hegna & Ren (2010) emphasized that the relative lengths of endites and endopods in the anterior cephalic limbs are diagnostic characters, which would exclude incompletely preserved fossil material from being determinable to genus. However, the Cretaceous genera have other characters that distinguish them from *Triops*: *Chenops* has a relatively long carapace and a large anal plate that clearly distinguishes the telson from that seen in species of *Triops*, and the labrum has a longitudinally extended shape. *Jeholops* is characterized by a subreniform dorsal carapace with gently curved posterolateral tips and a telson with subtrapezoidal outline. We emphasize that these differences allow a differentiation at the genus level. In how far they provide clues for the phylogenetic development and the relationship between the Triopsidae and other calmanostracans is a problem that was discussed in brief by Hegna & Ren (2010).

A third taxon of notostracans from the Lower Cretaceous Yixian Formation of north-eastern China has been described under the (parataxonomic, or 'supraspecific') name *Notostraca oleseni* Wagner *et al.*, 2019. The species is characterized by a carapace with a roundish outline covering two-thirds of the body (excluding furcal rami) and with rounded posterolateral corners. The anterior trunk region bears anterior thoracopods, and the middle trunk region bears a series of posterior thoracopods with several pairs of appendages per segment. The posterior trunk terminates in a subtrapezoidal telson with two elongated furcal rami. The discussion of Wagner *et al.* (2019) proposed this new taxon while specifically declining (p. 13) to examine the potentially conspecific taxa already described in the Chinese-language literature. This is an inadequate taxonomic practice. It should be noted that the Jurassic–Cretaceous of northeastern China (containing both the Jehol and Yanliao biotas) almost certainly has an unexplored relationship to sites in the coeval Transbaikal region in Russia (Bugdaeva & Markevich 2012).

Examination of the Voltzia Sandstone material for the analysis by Hegna (2012) and our subsequent examination shows that most of the notostracan specimens from the Voltzia Sandstone Formation belong to a single species. This species differs unequivocally from *Triops cancriformis* to which the material has been assigned by the earlier authors (Gall 1971; Pollard 1985; Kelber 1999; Gall & Grauvogel-Stamm 2005). In addition, this species also differs from the material from the Keuper beds of the Steigerwald region of Franconia described by Trusheim (1938) as *Triops cancriformis minor* (albeit Trusheim's original specimens are nearly all lost and the precise morphology is difficult to reconstruct), and it differs in a number of aspects from the subsequently collected specimens from the Keuper beds of the Hassberge region (Kelber 1998a, 1999), as will be shown in a separate study. This dominant calmanostracan species of the Voltzia Sandstone has the general morphology of the Recent species of the genus *Triops* (e.g. Linder 1952; Fryer 1988). However, significant differences can be seen in the relatively small eye tubercle with suboval compound eyes, the lack of a differentiated first antenniform thoracic appendage, *c.* 17–20 posterior limbs on the anterior trunk, a larger number of abdominal segments, and a subquadrate telson with minute spines on its posterior margin. For this genus and species, the original name *Apudites antiquus* of Schimper (1853) is available and revived here. Two other genera and species of branchiopods from the Grauvogel collection can be identified: one by its laterally compressed carapace and the other by its bivalved carapace. These represent a non-calmanostracan phyllopod and a diplostracan introduced here as *Olesenocaris galli* and *Grauvogelocaris alsatica*, respectively.

Family UNCERTAIN

Remarks. The suprageneric subdivision of the Notostraca is completely deficient of any robust concept; and this is even more true when the fossil record is considered. The family Triopsidae was introduced by Keilhack (1909), but on occasion erroneously assigned to Montalenti (1935). A superfamily Triopsoidea was introduced by Novojilov (1960) (but also ascribed to Montalenti 1935), and the family Apodidae Ruedemann, 1922 as replacing the Triopsidae Montalenti, 1935.

Although the Triopsidae received fairly great attention during the last decades, no robust concept of the family exists to date and no diagnosis has been proposed. The only exception is an emendation by Yang & Hong (1980), who suggested that the Triopsidae (erroneously assigned to 'Martalent 1935' as authority) include genera and species with a single eye, a carapace with a denticulate posterior notch, and a trunk differentiated into anterior and posterior portions (slightly rephrased here). Yang & Hong (1980) almost certainly meant that the two eyes were spatially restricted to the central eye tubercle (see their fig. 2), which indeed is a valuable character that unites phylogenetically younger notostracan taxa. However, denticles along the margin of the carapace cannot be regarded as a principal character (in the fossil record, denticles may not always be preserved), and it remains unknown how Yang & Hong (1980) tended to define the differentiation of the abdomen.

Recent studies on fossil notostracans concentrated on the shape of the carapace and presented them in morphometric analyses and morphospace diagrams (Wagner *et al.* 2017, 2019). However, the shape/outline of the carapace is of tertiary significance for notostracans phylogeny and even morphometric gradients of it cannot be taken for crucial indicators to elucidate taxonomic entities. More important are features such as the number and diversification of the trunk limbs; the presence or absence of appendages on the trunk; the development of the ventral subfrontal plate and labrum with adjacent mandibles; and the morphology of the eye tubercle.

Genus *Apudites* Schimper, 1853

Type species. *Apudites antiquus* Schimper, 1853.

Included species. Species tentatively assigned to *Apudites*: *Triops cancriformis minor* Trusheim, 1938.

Diagnosis. Notostracan genus with carapace subelliptical in outline, covering about two-thirds of the main body (exclusive of furcal rami), with posterior sulcus considerably indented, posterolateral corners acute; eye tubercle relatively small and subcircular in outline, compound eyes fairly small, suboval; cervical groove developed with a curved course; subfrontal plate broad (sag.); labrum simple, undivided, subrectangular in outline; thorax with *c.* 11–13 pairs of biramous thoracopods, one per segment; anterior part of trunk with small phyllopodous appendages, two per segment; trunk composed of *c.* 28–32 segments; telson with subquadrate outline, its posterior margin slightly curved and with minute spines, with one pair of multiannulated furcal rami.

Remarks. *Apudites antiquus* characterizes the genus *Apudites* typified by a carapace that covers approximately two-thirds of the main body (exclusive of furcal rami) and with a considerable posterior indentation as well as moderately acute posterolateral corners. The eye tubercle is relatively small, but characteristically subcircular in outline. The compound eyes are small and suboval. A distinct cervical groove is visible, which describes a considerable sigmoid curvature. The ventral side shows a broad (sag.) subfrontal plate and a simple, subrectangular labrum. The thorax consists of *c.* 11–13 segments, each with a single pair of biramous thoracopods, which terminate in relatively broadly elliptical and obliquely backward-directed flabelliform exopodites. The anterior part of the trunk carries small phyllopodous appendages, two per segment, regularly decreasing in transverse width rearwards. The trunk is composed of *c.* 28–32 segments, ending in a telson with a subquadrate outline and a pair of multiannulated furcal rami. The posterior margin of the telson is slightly curved, with a series of minute spines projecting rearward from the margin.

This *Apudites* morphology can be estimated as paradigmatic for the early Mesozoic character set, particularly in respect to the number of thoracic and abdominal segments; the broad exopodites of the thoracopods; the numerous rearwardly decreasing phyllopodous appendages at the anterior part of the trunk; and a subquadrate and poorly subdivided telson. Particularly characteristic is the subcircular eye tubercle with the two oval compound eyes. This feature clearly distinguishes *Apudites* from earlier notostracans such as *Strudops* Lagebro *et al.*, 2015, which has a much smaller dorsal organ as a probable precursor of the later well-developed eye tubercles. Additional differences are the much shorter trunk and the subrectangular to slightly trapezoidal outline of the telson in *Strudops*.

Lynceites Goldenberg, 1870 is known from two species. Its type species, *L. ornatus* Goldenberg, 1870 from the Stephanian of the Saar Basin and Thuringia, Germany, is characterized by a well-developed and crest-like carina on the carapace, a minute 'eye tubercle' apparently composed only of a singular dorsal organ, a mandibular bulge, and the tendency to develop less clearly curved posterolateral margins of the carapace. A second species, *L. cansoensis* Copeland, 1957, from the Namurian Canso Group of Maritime Canada, is known only from isolated carapaces with a distinctly more elongate outline, a low curvature of the anterior margin of the carapace, extended posterolateral corners, and a low, poorly developed mandibular bulge so that its genus-level affinity must be regarded as unresolved. It shares with *L. ornatus* the distinct median ridge and the minute eye tubercle.

Heidiops Werneburg & Schneider, 2023 is also distinguished from *Apudites antiquus* by a trunk with fewer segments. Its carapace is subelliptical in outline (except for the posterior recess), often with a unique dorsal sculpture preserved, and it has a distinctly elevated carina extending to the margin of the indentation where it ends at a small but marked notch. Furthermore, the mandibular bulge of *Heidiops* has strong hemispherical distal edges where the mandibles would have articulated.

Notostracans from the Coburg Sandstone (Hassberge Formation) of the Steigerwald region in Franconia, Germany, have been described under the name *Triops cancriformis minor* Trusheim, 1938 and were the first to extend the range of the Recent species *Triops cancriformis* into Triassic strata. The rich material of excellently preserved specimens was never adequately re-studied after Trusheim's (1938) short article, meaning that particular details of the anterior trunk and the telson are unidentified. Unfortunately, most of Trusheim's specimens appear to be lost and additional material cannot be collected from the type locality, therefore these characters remain uncertain. Nevertheless, the Steigerwald specimens differ from *Apudites antiquus* in a number of characters: the carapace has a more anteriorly extending recess so that the posterolateral corners are distinctly more sharply developed (Trusheim 1938, pl. 13, figs 2, 3), a character that also separates the Steigerwald specimens from the Hassberge specimens, which are usually regarded as conspecific with Trusheim's (sub)species (e.g. Kelber 1998a, 1999; Wagner *et al.* 2017, 2019). The number of trunk segments is not exactly known, but according to Trusheim's figures and analogous specimens from the Hassberge region it probably lies around 25–30. The specimens of Trusheim's samples have smaller mandibles with a more strongly elliptical outline. The limbs at the anterior trunk segments appear to have been larger (Trusheim 1938, pl. 14, fig. 3). Despite Trusheim's reconstruction (1938, figs 1, 7), the evidence for *Triops cancriformis minor* possessing modern-style elongate, antennaeform endites on its first post-cephalic appendages is equivocal. Trusheim's (1938) plate 13.5 seems to suggest they are absent, while plate 14.3 may bear a trace of them in the upper left corner (with arrow). The telson is known only from a single figured specimen in Trusheim (1938, pl. 13, fig. 4). This specimen shows a telson with a slightly transverse subrectangular outline and obliquely truncated posterolateral margins as well as two pits, which Trusheim (1938, p. 216) emphasized and described them to be 'surrounded by bristles'. This configuration seems to have led him towards the reconstruction (Trusheim 1938, fig. 1) that very much resembles the morphology of the extant species *Triops cancriformis*. These characters clearly distinguish *Triops cancriformis minor* on a species level from *Apudites antiquus*, but the species are possibly related in a way that they might represent the same genus. Nevertheless, a robust assignment requires a better knowledge of diagnostic characters therefore we only tentatively suggest that this species belongs to *Apudites*.

Two Notostraca have been described from the Lower Triassic Liujagou Formation of the eastern Ordos Basin, northern China, under the names *Discocephala jiaochengensis* Hong, 1985 and *Dikelocephala peijiashanensis* Hong, 1985. The two species involve some nomenclatural imbroglio: they were first used in a regional palaeontological atlas (Yang & Hong 1984). In that atlas, the authority was cited as 'Hong, 1984,' but they were not introduced as new taxa. Furthermore, no paper by Hong, dealing with branchiopod crustaceans, was published in 1984. They were formally introduced in a study by Hong, which was published in 1985. It seems that the 1984 atlas beat the 1985 study to publication. In Hong's (1985) study, they were also spelled and cited as *Discocephala jiaochengensis* (with alternative spellings of the genus name, *Dicocephala* and *Discokephala*, also appearing in the paper) and *Dikelocephala peijiashanensis*. The two genera and species were separated by Hong (1985) from the Triopsidae under the newly erected family Discocephalidae, but without providing any characters for the distinction. Without differentiating characteristics, both species should now be regarded as synonyms, with *Discocephala jiaochengensis* taking priority due to it being named first in the original paper (Hong 1985).

This genus and species are characterized by a carapace that has a subcircular outline except for a considerably indented posterior sulcus with a nearly even curvature. The eye tubercle is subcircular and similar in size, outline and position to that of *Apudites antiquus*, and the subfrontal plate is similar in shape and size. However, the preservation of these notostracans from North China does not allow precise recognition of additional important characters of the carapace, the anterior trunk and the telson (Hong 1985, pl. 60, figs 1–5). Nevertheless, the posterior trunk unmistakeably distinguishes *Discocephala jiaochengensis* from *Apudites antiquus*: the part of the body that extends rearward from below the carapace is clearly longer than the carapace, wider, distinctly tapering and composed of many more segments. It seems as if it ends in a single massive thorn but it is more probable that an originally developed pair of caudal furca fell off after the death of the specimen.

Soergel (1928) described notostracans from the Lower Triassic Buntsandstein of Thuringia in much detail. He assigned them to the genus *Apudites*, but left them in open nomenclature with regards to species. These specimens were found in the Thüringischer Chirotherium-Sandstein (lower part of Röt Formation) and are only slightly older than the specimens of *Apudites antiquus* from the Voltzia Sandstone. The material is preserved in sandstone and thus offers only a few imprecise morphological details. However, an elliptical shape of the carapace with a narrow curvature of the anterior tip; an unusually large eye tubercle located close to the anterior tip of the carapace; long and well-developed maxillary gland marks; and a long abdomen of roughly equal length as the carapace, clearly distinguish this unnamed species from *Apudites antiquus* and all other formally introduced Permian and Triassic notostracans.

Gore (1986) described a notostracan from the Rhaetian (or Norian?) of the Newark Supergroup of the Culpeper Basin of Virginia, which she determined as *Triops* cf. *cancriformis*. Gore (1986) emphasized that the Culpeper Basin notostracans have a rudimentary supra-anal plate (visible in Gore 1986, fig. 3.1). Re-imaging of Gore's (1986) figured and unfigured material failed to show any sort of supra-anal plate; the specimen in Gore's figure 3.1 has a scratch between the caudal furca. The carapace also has a similar shape to that of *A. antiquus*, but is clearly distinguished by a narrower posterior indentation with a notch-like incision of its margin on the sagittal line. Unfortunately, the eye tubercle is poorly known in the Virginia material, although two specimens show a subcircular structure with an apparently quite well-developed pair of semicircular compound eyes and a slight posterior indentation of the eye tubercle (Gore 1986, figs 3.7, 3.8). It should be noted that today, *Triops cancriformis* is found only in Eurasia and north Africa, whereas several different species of *Triops* are found in North America. If Gore's identification of the fossils as *Triops* cf. *cancriformis* is correct, it would suggest a previously unrecognized biogeographic range shift. In summary, the specimens from the Newark Supergroup of the Culpeper Basin possibly represent a species, which may be placed under *Apudites* according to the known characters, pending formal description of a species (TA Hegna, unpub. data, 2024).

Ellenberger (1970) introduced a new species of notostracans under the name '*Apodites phuthingensis*' and mentioned another one under the name '*Apodidites* (?)', as well as questionable notostracan fragments assigned to 'Apodidés (ou peut-être des Anaspidacea?)' ('Apodids (or perhaps Anaspidacea)'), all from the uppermost Upper Triassic to Lower Jurassic Stormberg Group of Lesotho. However, the preliminary paper does not contain any figures or further data therefore the mentions must be regarded as *nomina nuda* and unreliable data.

Apudites antiquus Schimper, 1853
Figures 2–7

1840 *Apus antiquus* Schimper, p. 338
* 1853 *Apudites antiquus* Schimper, pp. 7–8, pl. 3, unnumbered lower three figures.
1864 *Apudites antiquus*. W. P. Schimper; Alberti, p. 193.
1914 *Apudites antiquus* Schimp.; Bill, pp. 325, 331.
1928 *Apudites antiquus* Schimper; Schmidt, p. 313, fig. 858 (upper left and right specimen only).
1928 *Apudites antiquus*; Soergel, p. 29.
non 1928 *Apudites* sp. Soergel, pl. 1, figs 1–11, pl. 3, figs 1–6, pl. 4, figs 1, 2.
1936 *Apudites antiquus* Schimp.; Firtion, p. 17.
1938 '*Apudites*' *antiquus* Schimper; Trusheim, pp. 209, 210.
1938 *Triops antiquus* (Schimper); Trusheim, p. 210.
1938 *Triops antiquus* Schimp.; Schmidt, pp. 46, 112, fig. 858a.
1940 *Apudites antiquus* Schimper; Chernyshev, pp. 6–7.
1953 *Apudites antiquus* Schimper; Dechaseaux, pp. 260–261.
non 1969 *Apudites antiquus* Schimper; Jörg, p. 87.
1969 *Triops cancriformis*; Tasch, pp. R134–R135 (*pars*).
1971 *Triops cancriformis*; Gall, pp. 36, 39, 128 (*pars*).
1971 *Triops cancriformis minor* Trusheim; Gall, pp. 38–39, 82, 121, tables 1, 8, pl. 7, figs 3, 4 (only).
non 1971 *Triops cancriformis minor* Trusheim; Gall, p. 309, text-fig. 6.
1993 *Triops*; Gall & Grauvogel-Stamm, pp. 143, 145, table 2.
1997 *Apudites antiquus* Schimper; Gand *et al*., p. 696.
2005 *Triops cancriformis*. Gall & Grauvogel-Stamm, pp. 637, 638, 641, 649, table 1.
2005 *Triops* (*Apus*) *cancriformis* (Schaeffer); Gall & Grauvogel-Stamm, p. 647.
2006 *Triops cancriformis*. Gall *et al*., p. 26 (middle right column image only).

Neotype (chosen herein). Specimen SMNS 75644-18a (= Grauvogel's cat. no. Ap2a).

Type locality & type stratum. Schimper (1853) did not provide any precise information on the origin of the specimens described by him from the 'grès bigarré' (= Buntsandstein, Lower Triassic). However, it is certain that they have been collected from the Grès à meules member of the Voltzia Sandstone, from a quarry near Soultz-les-Bains, Vosges. The neotype was collected by Louis Grauvogel from the Grès à meules member of the Voltzia Sandstone, from a quarry near Soultz-les-Bains as well.

Studied material. SMNS 75644-1 (original catalogue number Ap13 of previous publications), SMNS 75644-2a, b (=Ap14; part and counterpart), SMNS 75644-3a, b (=Ap12; part and counterpart), SMNS 75644-4a, b (=Ap11; part and counterpart), SMNS 75644-5a, b (=Ap23; part and counterpart), SMNS 75644-6a, b (=Ap15; part and counterpart), SMNS 75644-7a, b (=Ap16; part and counterpart), SMNS 75644-8a, b (=Ap9; part and counterpart), SMNS 75644-9a, b (=Ap10; part and counterpart), SMNS 75644-10a, b (=Ap19; part and counterpart), SMNS 75644-11 (=Ap18), SMNS 75644-12 (=Ap8), SMNS 75644–13 (=Ap7), SMNS 75644-14 (=Ap20), SMNS 75644-15a, b (=Ap21; part and counterpart), SMNS 75644-16 (=Ap22), SMNS 75644-17a, b (=Ap17; part and counterpart), SMNS 75644-18a, b (=Ap2; part and counterpart), SMNS 75644-19a, b (=Ap3; part and counterpart), SMNS 75644-20 (=Ap4), SMNS 75645-5a.

Diagnosis. Species of *Apudites* with a carapace of *c.* 60% maximum body length (except caudal rami) and a width *c.* 85–90% of length; sulcus moderately indented with a faint spike developed at midline.

Description

General morphology. The chitinous, slightly sclerotized dorsal carapace (Fig. 2) covers the cephalon, the thorax, and the anterior part of the abdomen, but the remaining part is well exposed (e.g. Figs 2F, 3–5). Some of the studied specimens of *Apudites antiquus* allow a count of the number of segments with sufficient precision for the present species due to preserved ventral segmentation. The number of segments varies slightly among the specimens, which is interpreted as being a result of different ages of the individuals. In total, *c.* 40–45 segments can be counted. The number of the post-cephalic thoracopod-bearing thoracic segments is 11–12, possibly even 13 (e.g. Figs 3C, 4A, C, 5A–C). Probably 17–20 segments with limbs are present in the posterior trunk, interpreted to carry two blade-shaped appendages (equivalent to the 'abdominal feet' of the older literature) (e.g. Fig. 4C). The exact boundary between anterior, limb-bearing abdominal segments and the legless posterior abdomen is difficult to determine in most specimens, but occasionally recognizable and lies approximately at the level of the spine tips of the carapace (Figs 3A, 4C, 5A). The (assumed) post-thoracic part of the trunk consists of *c.* 28–32 segments in adult individuals and terminates with a telson and furca with two long caudal rami. The body size varies considerably between the specimens. Normal-sized, complete specimens range in length from 4.5 mm (SMNS 75644-5b; Fig. 6C) to 7 mm (SMNS 75644–7; Fig. 3A), *c.* 8 mm (SMNS 75644-18b; Fig. 3C) and 8.5 mm (SMNS 75644-18a; Fig. 4A) from the anterior margin of the carapace to the posterior tips of the furca. The largest known carapace (SMNS 74644-2a; Fig. 2B) is *c.* 9.5 mm long, whereas the smallest carapaces from the Grauvogel collection are only 2.5 mm in length. The largest specimen is represented by a partial trunk with attached telson of *c.* 5.5 mm in length, suggesting a length of *c.* 20 mm for the complete specimen (including the furca).

Dorsal carapace. The cephalothoracic shield of *Apudites antiquus* is a distinctly convex structure deriving from the fusion of the head shield and the carapace fold originating from the maxillary

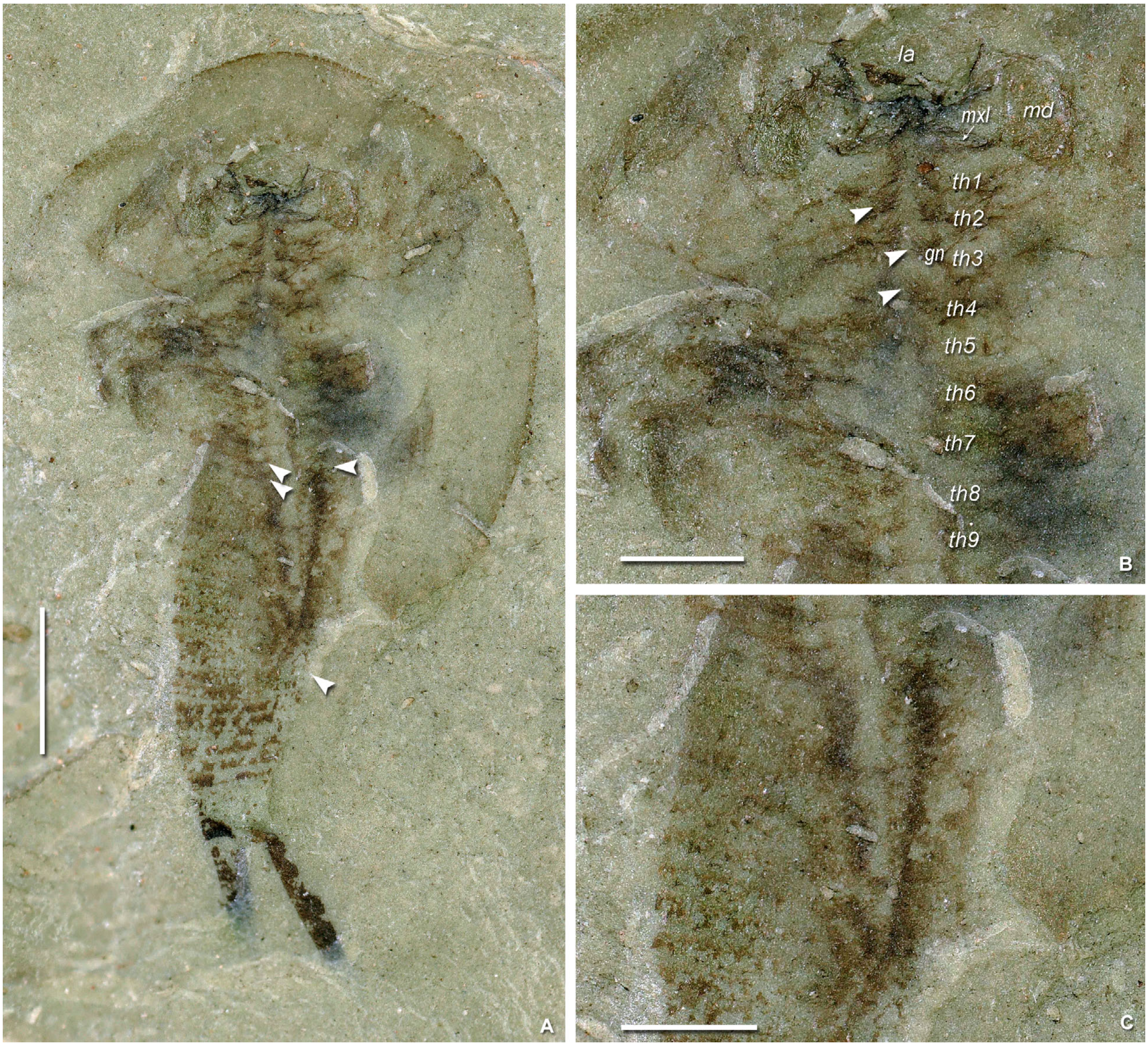

FIG. 3. *Apudites antiquus* Schimper, 1853; SMNS 75644-7a. A, entire specimen, ventral view with partly preserved ventral appendages and laterally shifted food groove (arrows), with the posterior limbs visible as v-shaped area with subparallel cross-sections of the lamellar flabella. B, magnified view showing labrum and remnants of limbs, particularly the gnathobases with obliquely anteriorly directed bristles (arrows); note mineralized parts (black threads) of muscles between mandibles and transversely directed maxillula(?). C, magnified view showing v-shaped area with subparallel cross-sections of the lamellar flabella. *Abbreviations*: gn, gnathobase; la, labrum; md, mandible; mxl, maxillula; th1–9, thoracopods 1–9. Scale bars represent: 1 mm (A); 500 μm (B, C).

segment (Fryer 1996). It has a gently curved anterior margin and less curved lateral margins. The posterior margin described a conspicuous sulcus between a pair of more-or-less distinctly rearwardly extended spines of different size. The ratio of the sagittal length of the carapace (up to the tips of the posterolateral spines) to the maximum body length (except caudal rami) is *c.* 55–62%. The width/length ratio of the carapace ranges between 74% and 93% in the studied specimens, frequently being reduced by slight lateral compaction. The course of the posterior sulcus is generally a moderately wide (tr.) and moderately curved recess (or notch). The course is often somewhat modified due to the dorsoventral compaction and nearly complete flattening of the originally convex shield, which may result in nearly subparallel extreme sections of the lateral margins of the recess in front of the posterolateral spines (Fig. 2A, D–E) or a gentle double composite arc with a notch on the sagittal line (e.g. Figs 2A, 5A). The precise course of this posterior margin and the distinctness and expression of the median notch is affected by the taphonomic history of the specimen: the relative width of the recess in relationship to its depth (sag.) is increased if the carapace underwent a distinct dorsoventral compression during early diagenetic compaction of the sediment. Minute spines or bristles are arranged as a series at the edge

FIG. 4. *Apudites antiquus* Schimper, 1853. A–C, SMNS 75644-18a, neotype: A, entire specimen, dorsal view showing most of the ventral appendages. B, magnified view of right thoracic region with remnants of thoracopods with gnathobases/protopodites, second endite and bristles on the endopodite and exopods (arrow/labelled). C, detail of posterior thoracic and abdominal regions, with the posterior trunk limbs visible as subparallel cross-sections of the flabella (arrows in the central part of the photo). *Abbreviations*: en2, second endite; epd, endopodite; et, eye tubercle; ex, exopod; gn, protopodites with gnathobase; la, labrum; md, mandible; th1–11, thoracopods 1–11. Scale bars represent: 1 mm (A); 500 μm (B, C).

of the sulcus, but these are preserved in only some of the specimens, in which this edge of the sulcus is serrated with numerous small spine-like nodes (Fig. 2C–D, arrows). A very thin doublure along the rim of the sulcus is developed on its ventral side.

The attachment of the cephalon to the carapace is limited to a relatively narrow transverse strip, which is usually not visible in the fossil material, but is marked in one of the studied specimens (Fig. 2F).

The eye tubercle in *Apudites antiquus* is moderately large and subcircular in outline, with a minute indentation at the posterior margin (Fig. 2A–B). It includes two suboval compound eyes of relatively small size located close to each other and *c.* 10% of the sagittal carapace length from the anterior margin. Not recognized in the specimens are the median naupliar eye and a nuchal organ (also termed dorsal organ). However, a structure that may indicate the position of the naupliar eye is recognizable in SMNS

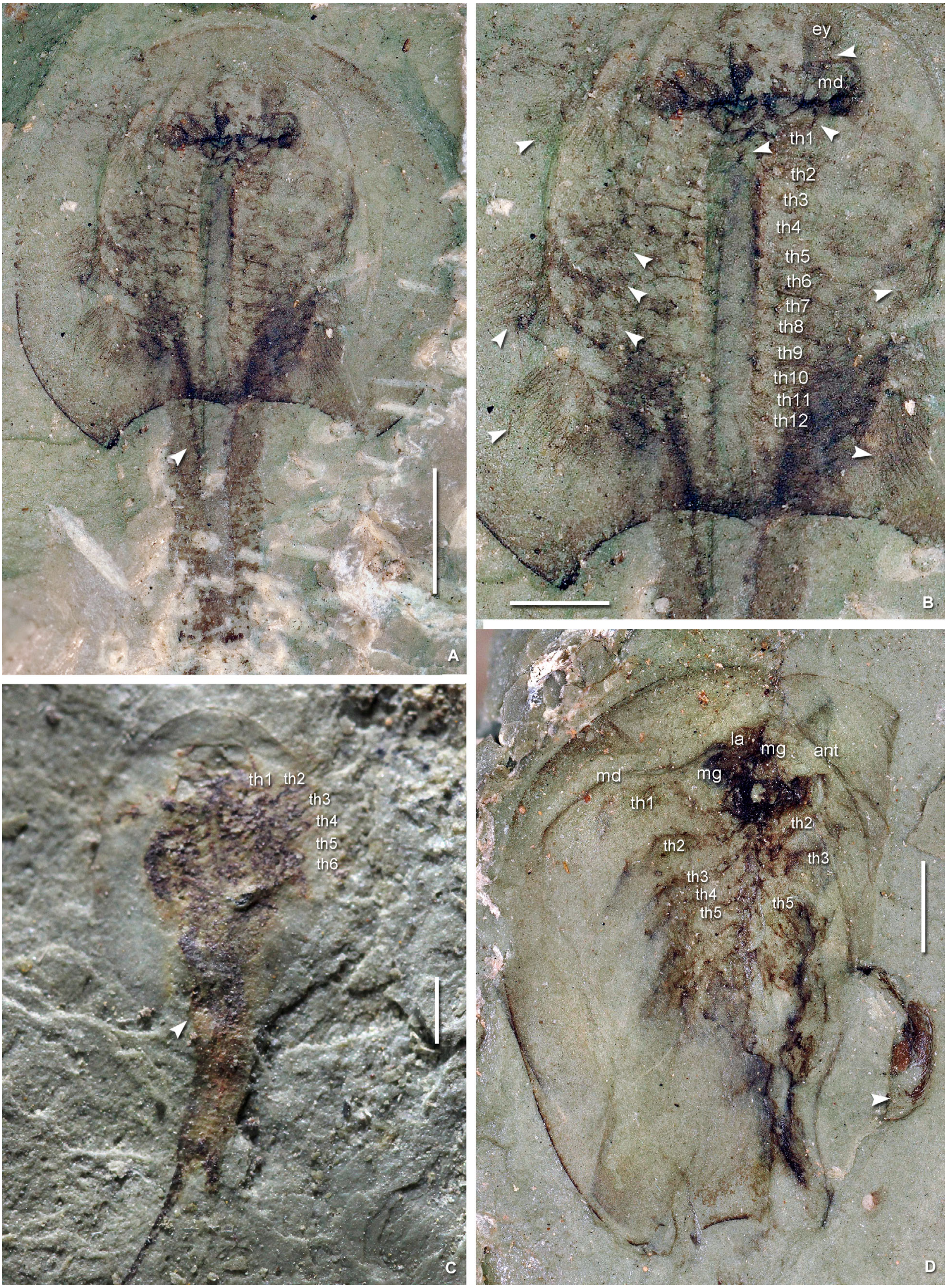
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FIG. 5. *Apudites antiquus* Schimper, 1853. A–B, SMNS 75644-6a: A, entire specimen, with distinctly visible series of posterior trunk limbs (arrow); B, magnified view of cephalic and thoracic regions with remnants of thoracopods with preserved bristles on various exopods and endites; note also vestiges of tissue fibres next to right eye (arrow). C, SMNS 75645-5a, incomplete specimen, dorsal view, with imperfectly preserved, partly lengthened ventral appendages (labelled); position of most posteriorly located appendages indicated by arrow. D, SMNS 75644-3a, incomplete, slightly deformed carapace with remnants of ventral appendages, ventral view; note slight fold that marks the margin of the cephalic doublure (md), anteriorly shifted right maxillar gland (mg) and first thoracopod (th1); arrow points to unidentified partially preserved arthropod. *Abbreviations*. ant, antenna; ey, eye; la, labrum; th1–12, thoracopods 1–12. Scale bars represent: 1 mm (A, C); 500 μm (B, D).

FIG. 6. *Apudites antiquus* Schimper, 1853. A, SMNS 75644-19b, telson and caudal rami (slightly detached), showing small thorn-like spines at the posterior margin of the telson and at posterolateral edge (arrows). B, SMNS 75644-1c, isolated posterior trunk (composed of 17 segments) and telson with sharp, rearwardly directed spines. C, SMNS 75644-5b, nearly complete specimen preserved in progressive stage of decay such that the ventral appendages underneath the carapace are preserved as a brown ramified mass, whereas the relatively broad gut track is recognizable in part of the thorax and abdomen (arrow). Scale bars represent: 500 μm (A); 1 mm (B); 2 mm (C).

75664-8a. A shallow and indistinct transverse groove (nuchal or mandibular groove) is developed on the carapace. An additional, more extended groove with a distinctly curved course lies posterior to it and is usually termed the cervical groove. The posterior two-thirds of the carapace are separated on the sagittal line by a more-or-less distinct crest-like rim termed the 'carina', which is smooth and without any recognizable spines along its course (Fig. 2F–G). This carina is not preserved in strongly flattened and demineralized specimens, which accounts for most of the collected specimens from the Voltzia Sandstone localities.

A pair of extended, roughly kidney-shaped shallow depressions is usually seen in the recent species of *Triops* and marked the extension of the maxillary glands. This feature is only vaguely indicated in the studied specimens and marked as remnants of a pair of rather sausage-shaped, smooth fields (Fig. 2A–B), but this is again a result of the taphonomic overprinting of the specimens' original morphology. Similar structures are observed in some, but not all, fossil notostracans. Whether this is due to unknown factors affecting the maxillary glands, or some species simply having more prominent maxillary glands, is unknown.

Cephalic & thoracic ventral anatomy. Ventrally, the carapace cuticle folds under the head, making a frontal doublure. This frontal doublure pinches out laterally, giving it a crescent shape. Medially, this serves as the point of attachment for the labrum. The labrum has a subrectangular to slightly subpentagonal outline with a distinctly elevated subcentral region (Figs 3B, 4A).

Vestiges of the antennas are not recognized with certainty in any of the specimens of *Apudites antiquus*. Specimen SMNS 75644-3a (Fig. 5D, md) appears to show a long antenna on the left (anatomically dextral) side apparently developed in the usual uniramous manner. However, we interpret this as the margin of the cephalic doublure attached to the labrum.

In contrast, the mandibular region is frequently visible and preserved in different styles: more-or-less three-dimensionally preserved carapaces show a transverse mandibular bulge with a strongly lobate middle portion (as seen in other Triassic notostracans) and moderately large lateral extensions (Fig. 2B) that indicate the location of the mandibular articulation. The size of the mandibular articulations seems narrower than in modern notostracans. The paired mandibles are seen in most of the specimens with preserved soft-parts, usually as dark subtriangular areas that appear to represent the mandible coxal bodies, connected by thin dark threads with the centrally located anterior part of the food groove and alimentary canal area, which is also generally preserved as a dark band (Figs 3A–B, 4A, 5A–B, D). However, no details of the mesial edges of the mandibles can be identified. A particularly instructive specimen (SMNS 75644-7a; Fig. 3A–B) shows the mandibles slightly rotated from the normal life position with the distal edge shifted posterolaterally relative to the labrum, connected by muscles that are indicated by dark threads (compare with Zaddach 1841, pl. 1), and with the maxillula preserved in a transverse position (Fig. 3B).

The thorax in *Triops* and morphologically similar taxa has been differently treated during scientific history, and we here restrict the thorax to the part of the body that has sometimes been referred to as the anterior thorax and is characterized by large thoracopods branched into well-differentiated endites and with a sophisticated set of setae. The break between anterior thorax and posterior thorax (anterior abdomen) in modern notostracans is the location of the egg-carrying eleventh limbs; after this, the limbs of both sexes shift in morphology (the endopod becomes lobate and the exopod becomes rounded). The posterior thorax of previous studies constitutes the anterior part of the abdomen and is typified by smaller, narrowly spaced posterior limbs without endites and without well-developed setae. This thorax consists of 11 segments in the Recent notostracans. The studied specimens of *Apudites antiquus* from the Voltzia Sandstone localities have between 11 and 13 thoracopods in the anterior part of the trunk, with one pair at each segment.

In modern notostracans, each of these appendages consists of a protopodite, a small endopodite, a larger exopodite, and a suboval epipodite (gill). Five small endites, similar in shape to the endopodite, are present in Recent triopsids. However, these details were not known with certainty from any of the fossil species assigned to *Triops* to date. A median ventral food groove lies between the thoracic limbs and the sterna of the thoracic segments. This groove is rarely preserved in a representative way, but the lateral boundaries can be recognized by the dark carbonaceous trace caused by the overlain spines of the gnathobases on either side (Figs 3A–B, 4A–B), occasionally grading upward into the level of the digestive tract when the plane lies slightly obliquely to the axis of the body (Fig. 5D). The relatively robust bristles on the gnathobases are occasionally preserved individually, such as in specimen SMNS 75644-7a, where they are recognizable as obliquely forward-directed tufts (Fig. 3B).

No precise details on the morphology of the thoracopods can be recognized in the studied specimens of *Apudites antiquus*, but several of the specimens show vestiges of some of the exopods and endites together with remains of the setae. Distinctive parts of the thoracopods are differentiated in some specimens (visible most typically in SMNS 75644-18a; Fig. 4). The protopodites (or first endites) are commonly preserved as dark areas near the food groove, and they show thorn-shaped anterolateral extensions in SMNS 75644-18a (Fig. 4B, anterior arrows), with the second endite sometimes recognizable. The same specimen nicely exhibits long lamellae on the posterior margin of the exopodites (e.g. Figs 4, 5A–B). These exopodites appear to have been more broadly developed than in Recent species of *Triops*, but also less extended and less rearward directed.

The first trunk limb, or thoracopod (th1) in the Recent species *Triops* is known to have a particular anatomy with two long and two smaller annulated antenniform 'feelers' (distal endites) that arise from the protopodite. The first endopodite, in contrast, is very reduced. None of the studied specimens of *Apudites antiquus* shows such extended limbs. Given that these are known to be relatively robust and are preserved during decay experiments (Hegna 2012), such extended antenniform limbs almost certainly were not developed in *Apudites antiquus*.

The dark colouration results from an early diagenetic staining by organic substances due to a pronounced decay triggered by microbial activity, and its concentration around the midline is explained as resulting from the relatively massive gnathobases/protopodites, but the amount of staining differs significantly and can affect different amounts of the tissue (compare Figs 3A–B, 6B–C, 7A). The central area with the protopodites and its processes can also be preserved as a slightly raised subrectangular area on the dorsal carapace when imprinted through this shield. Occasionally, specimens show an individual preservation of partial limbs, often not aligned parallel to each other (e.g. Figs 3B, 4B). This suggests some amount of decay prior to preservation, given that the ventral cuticle would only be able to shift like that after the loss of internal tissues (i.e. muscles).

No egg-carrying appendages or eggs have been identified in any of the specimens.

Trunk/abdomen inclusive of telson. In Recent species of *Triops* the trunk consists of two types of segments: those with tiny posterior limbs covered with incomplete chitinous rings with a central gap on the ventral side; and those without limbs, which are ring-like. The anterior part of the trunk is covered by the carapace (unless squeezed posteriorly during compaction).

The anterior part of the trunk in *Apudites antiquus* with its smaller phyllopodous limbs is recognizable in at least three of the studied specimens. It is characterized by a reduced sagittal length

FIG. 7. *Apudites antiquus* Schimper, 1853, part and counterpart. A, SMNS 75644-17b, nearly complete specimen fossilized under progressive stage of decay, with ventral appendages preserved as a dark brown mass, whereas the three-dimensionally preserved gut track is shifted laterally and recognizable in part of the thorax and abdomen. B, SMNS 75644-17a, nearly complete specimen fossilized under progressive stage of decay, with gut trace in differential preservation and not in life position (arrows). Scale bars represent 1 mm.

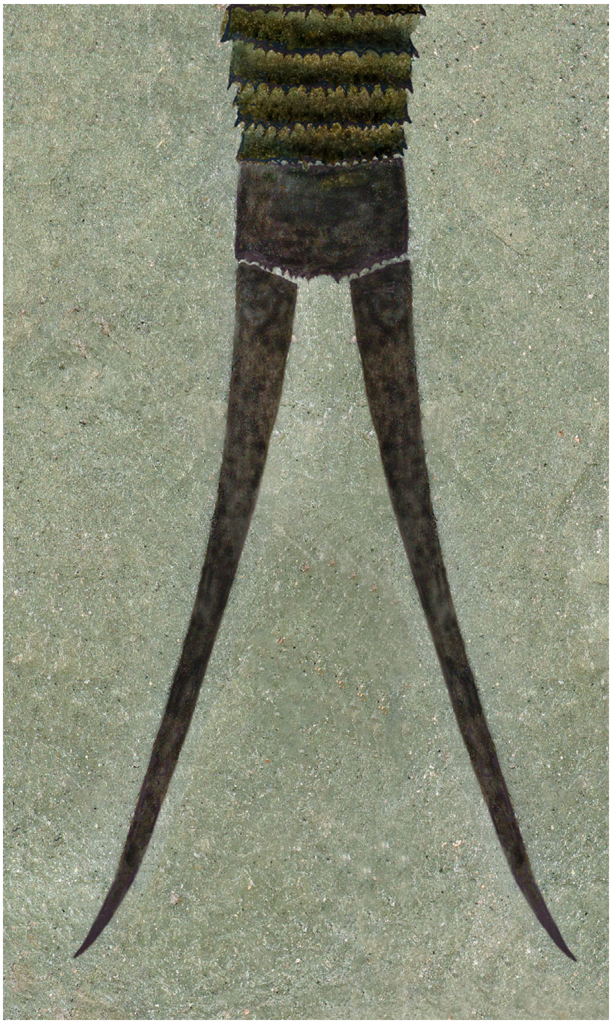

FIG. 8. *Apudites antiquus* Schimper, 1853. Reconstruction of the posterior trunk, telson and caudal rami based on several specimens (SMNS 75644-1c, SMNS 75645-5a, SMNS 75644-5b, SMNS 75644-7a, SMNS 75644-17a, SMNS 75644-18a, SMNS 75644-19b).

of the somites and shows an extended triangular outline of this functional unit (Figs 3A, 4A, C, 5A). These smaller limbs lose their correspondence to the regularly spaced abdominal segments and become more closely spaced, leading to the indistinct triangular area formed by the closely overlapping limbs. The number of somites lies in the order of 20–26 and appears to differ between individuals. The limbs cover a posteriorly decreasing minor part of the ventral surface. The narrowly spaced lamellar lobes are sometimes recognizable such as in SMNS 75644-18a, where they are preserved as subparallel cross-sections of the blades (Fig. 4C).

In the investigated material, the posterior part of the rings in the Voltzia Sandstone specimens is usually darker stained because of a higher amount of organic substance due to the overlap of adjacent rings and the connecting arthrodial membrane (Figs 2F, 7B). One specimen (SMNS 75644-7a, Fig. 3A, C) appears to have two segments that consist of a (right-handed) spiral of two rounds between two regular rings (similar to what has been observed in specimens of the extent *Triops longicaudatus*; Linder 1952). In addition, the rings carry moderately large, sharp, rearwardly directed spines on their circumference in the posterior half of the trunk, which project distinctly beyond the posterior margin of the rings (e.g. Fig. 7B). The rings are connected by a weak arthrodial membrane in life, but they can detach during early decay (Fig. 7B; see also Hegna 2012, fig. 19.4). The size of the trunk segments decreases successively in rearward direction, which creates a longitudinal conical outline in smaller specimens. The presence of the sharp backwardly directed spines on their circumference is connected with faint, longitudinally elongated shallow indentations around the spines, which may be preserved as narrow grooves in the specimens.

The trunk ends in a telson and two attached long annulated furcal rami (Fig. 8). The telson in *Apudites antiquus* shows a moderate morphologic plasticity, with a shape being slightly subrectangular to almost subquadrate in outline, but with a moderately curved posterior margin (Figs 2E, 5A, 6A). The lateral margins are nearly straight to slightly concave in dorsal view. The median sector of the posterior margin with its rearward curvature carries minute spines, particularly between the attachment sites of the rami, but also sometimes along the attachment sites, with the median spines being barely longer.

The caudal rami usually have a length of approximately two-thirds to three-quarters the length of the exposed part of the trunk, but appear to differ in length, and they are weakly to gently curved abaxially.

Digestive tract. The species of *Triops* are known to be omnivorous and to ferociously feed on nearly everything. Consequently, the digestive tract is largely filled with sediment particles of their immediate substrate. This robust filling provides a fairly good opportunity for the digestive tract to be fossilized. Accordingly, infillings of the digestive tract can be recognized in a number of the studied specimens. It is commonly preserved as a dorsoventrally compacted cylindrical body with smooth surfaces (Figs 6C, 7) but partly with segmentation imprinted on it as a carbonaceous stain. A special configuration is shown in Fig. 7B, where the thoracic section of the digestive track was obviously overprinted during early diagenetic processes and shows sack-like pouches whereas the abdominal section is preserved as a compacted cylindrical body. It cannot be ruled out, however, that this configuration is the result of a rupture of the digestive tract due to postmortem gas build-up by gut microbes. The sediment filling starts around the oral opening with the part underneath the labrum (Fig. 5B). In most cases, no difference appears to exist between the section included in the thorax and that in the abdomen.

Remarks. The first description of notostracan specimens from the Voltzia Sandstone Formation was published by Schimper (1853, pl. 3), who described them as *Apudites antiquus* (although he used the intended species epithet, *antiquus*, in an earlier report dated 1840), tacitly introducing a new genus and species. He accentuated differences with *Apus cancriformis*, thus recognizing that the Vosges specimens represented a different species, but explanations of the criteria of the newly erected genus *Apudites* are lacking. On his plate 3, Schimper (1853) correctly showed restoration of the species with a subquadrate, albeit slightly longitudinally extended telson, whereas the figures of the specimens to the right indicate a relatively short, transversely rectangular telson.

Neglected for many decades, *Apudites antiquus* was synonymized with *Triops cancriformis* (Bosc, 1801) without any explanation in a table published in Schmidt (1938), but then *expressis verbis* when the newly discovered specimens of Louis Grauvogel were described. This determination was influenced by the (at that time) brand-new discovery of specimens from the Keuper beds of Franconia (Trusheim 1938), with obvious differences not considered.

Apudites antiquus differs from extant species of *Triops* in the lack of differentiated first thoracic appendages (unlike the elongate, cheliped-like structure developed in *Triops*), a narrower mandibular bulge, a variable number of thoracic segments, a subspherical outline of the eye tubercle (contrasting with the mostly subreniform swelling in the species of *Triops*), a slightly extended subfrontal plate (Fig. 2F), and a telson with a subquadrate outline with a simple dorsal morphology (rather than the mostly transversely subrectangular outline with differentiated swellings and often conspicuous thorns seen in species of *Triops*). Indeed, the *Apudites antiquus* specimens examined in the course of this study have the same type of telson with a subquadrate outline as in the specimens from the Hassberge area described as *Triops cancriformis* or Notostraca *minor*, with slightly concave lateral margins and a moderately curved posterior margin, which carries small spines (Figs 2E, 5A, 6A, 8). These spines are slightly better developed in the median sector between the caudal rami, but do not reach a considerable size as in most of the Recent species of *Triops*. In any case, this telson is distinctly different from those of adults of the Recent specimens of *Triops cancriformis*, although juvenile specimens have a telson with a roughly similar outline, as well as other Recent species of *Triops*. In fact, none of the extant species is known to have such a telson in the adult condition, although specimens of *T. granarius* (Lucas, 1864) sometimes shows some resemblance, but lack the distinct median rearward curvature of the posterior margin. Indeed, the morphology of the telson inclusive of the configuration of the spines at the posterior margin and on the central area of the telson is regarded as among the most valuable criteria to distinguish the species (e.g. Longhurst 1955a).

The shape of the eye tubercle with its minute posterior indentation differs as well from that known from adults of all recent species of *Triops* and resembles more closely that of *Lepidurus batesoni* Longhurst, 1955a.

The carapace of *Apudites antiquus* is generally slightly subelliptical in outline (when the posterior recess is neglected) and slightly longer than wide. The posterior recess (or notch) of the carapace appears to vary considerably. However, a certain degree of the variation can be ascribed to a postmortem deformation during dorsoventral compaction as indicated by the slightly oblique course of the axis of symmetry (e.g. Fig. 4A). The normal condition in the extant species of *Triops* is a subevenly curved concave notch. However, compressed specimens have a more or less distinct acute process on the sagittal line, depending on the strength of the carina. Both conditions are developed in *Apudites antiquus*, similar to what Trusheim (1938, fig. 2) illustrated for the fossils from the Hassberge region.

The notostracan species discovered in Franconia was first described as *Triops cancriformis minor* by Trusheim (1938) and provided the base for the living fossil discussion and the subsequent assignment of the Voltzia Sandstone specimens to *Triops cancriformis* by Gall (1971). Unfortunately, Trusheim's (1938) significant original specimens from the Middle Keuper Coburg Sandstone (Hassberge Formation) of the Steigerwald region appear to be lost, and subsequently discovered specimens from the same formation in the Hassberge region (e.g. Kelber 1998a, 1999) require additional examination. Wagner *et al.* (2017) assumed that the specimens from both areas are identical and represent one species. Based on mainly the shape of the carapace, the authors concluded that this species cannot be assigned to *Triops* or *Triops cancriformis* in particular and suggested 'Notostraca *minor*' to avoid a traditional genus-level assignment. It needs to be emphasized, however, that the shape shown for 'Notostraca *minor*' in Wagner *et al.* (2019, fig. 3) is distinctly larger than in almost all specimens from the Hassberge and Steigerwald collections. Given that 'Notostraca', in this case, is not meant to be a genus name, it should not be italicized.

The abundant specimens collected from the Hassberge area are presently under (re)study by GG and KPK. As discussed above under the genus *Apudites*, the characters recognizable from Trusheim's (1938) figures and the few specimens available from the original locality suggest a close relationship with *Apudites antiquus*. However, the lack of information on some details, particularly the uncertainty on the precise morphology of telson in the type material from the Steigerwald area precludes a robust genus-level assignment. Accordingly, the species is best dealt with as *Apudites*? *minor* (Trusheim, 1938). The newly collected specimens from the Hassberge area predominantly have 13 thoracopods developed and thus more than *Apudites antiquus*. In addition, they have a similarly large and subcircular eye tubercle.

The affinities of specimens from the Upper Triassic Newark Group of Virginia (Gore 1986) have been discussed above, and are currently under restudy by TAH.

Two species assigned to *Triops* have been described from the Middle Jurassic of South China by Chen (1985), who underlined the similarity of *Triops hanshanensis* from the Hanshan Formation of the Anhui Province to Trusheim's *Triops cancriformis minor*. The species appears to occur in two morphotypes, with a slightly elongate carapace and a subelliptical carapace that is only a little longer than wide. However, the shape of the eye tubercles in the figured specimens (e.g. Chen 1985, pl. 1, figs 2, 4, 6) clearly indicates that the specimens underwent different degrees of longitudinal and lateral compression. The true original outline of the carapace appears to be subelliptical and similar to that known from the Hassberge area, and slightly more elongate than the shape of the carapace in *Apudites antiquus*. A character that clearly distinguishes '*Triops hanshanensis*' from *Apudites antiquus* and the species tentatively assigned to *Apudites* herein is the presence of a well-marked transverse sigmoidal mandibular groove on the carapace (e.g. Chen 1985, pl. 1, figs 4, 6). The posterior recess of the carapace in '*Triops hanshanensis*' is fairly narrow and restricted in its regional distribution, but describes a considerable arc in dorsal view. The dorsal carina is well developed and prominent. The eye tubercle is located relatively close to the anterior margin of the carapace. It is prominent and has a subcircular outline, with an apparently distinct dorsal organ at its centre. The compound eyes are kidney shaped. Unfortunately, details of the ventral and trunk anatomy are unknown except for a very large subfrontal plate that bears ridges along the posterior margin on either side of the labrum, and an extended part of the trunk that consists of 11 segments and a small telson without clearly recognizable features. These characters, particularly the eye tubercle and the mandibular groove as well as the distinct carina, suggest that the species represents a separate, not yet established genus.

Triops bashuensis Duan *in* Chen, 1985 was identified from the Shaximiao Formation in the Sichuan, Guizhou and Yunnan provinces, South China. As for '*Triops hanshanensis*' the species was interpreted to be represented by two morphotypes with different outlines of the carapace, which was attributed to a possible sexual dimorphism. In contrast to the specimens of '*Triops hanshanensis*' no clear indication for differential distortion is recognizable for the specimens of '*Triops bashuensis*', although the specimens show clear compaction-related features of deformation. The figured specimens indicate a surprisingly large range of variability in the shape of the carapace (with subcircular to distinctly longitudinally elongated carapaces) and particularly the posterior recess. However, there is a clear tendency that subcircular carapaces possess a relatively broad and shallow posterior indentation, whereas longitudinally elongate carapaces have a narrower and more indented indentation. Both forms show a distinct carina. They both have a transverse mandibular groove, but this groove is much less distinctly developed than in '*Triops hanshanensis*' and nearly straight or only slightly curved. The eye tubercle is almost spherical and prominent, with a narrow dorsal organ and a pair of kidney-shaped compound eyes. Interestingly, one specimen that shows the labrum and subfrontal plate has a significant bulge medially and anterior to the labrum; this feature has not been observed in any other notostracan, living or fossil. The absence of knowledge on the ventral appendages and the trunk does not allow a genus-level assignment of the species, which, however, cannot be assigned to *Triops* or *Apudites*.

Order DIPLOSTRACA Gerstaecker, 1866
Suborder & Family UNDETERMINED

Remarks. Two new phyllopod genera and species (introduced here as *Olesenocaris galli* and *Grauvogelocaris alsatica*) are associated with *Apudites antiquus* in the Voltzia Sandstone biota. Both are characterized by a folded, laterally compressed carapace; a trunk with numerous, weakly differentiated ventral appendages; a trunk composed of numerous segments devoid of appendages and extending considerably from below the carapace and exposed for most of its length; and a terminal body end with a telson and caudal rami. Superficially, both can (informally) be considered as crustaceans resembling the body of the upper Cambrian *Rehbachiella* Walossek, 1993, a stem-group representative of the branchiopod eucrustaceans (albeit interpreted as representing the anostracan lineage; Walossek 1993; Waloszek 2003). As for other representatives of phosphatized microarthropod remains of the Cambrian and Ordovician, however, the caveats regarding its semaphoront condition must be kept in mind.

The significant characters of both *Olesenocaris* and *Grauvogelocaris* are insufficient to assign them to an existing higher taxon. Recognizable features can even be alternatively interpreted. Features such as the absence of growth lines on the carapace and the long trunk could be understood as representing a basal phyllopodan or even a stem-calmanostracan. However, the majority of the morphological features of both genera and species suggests that they could be ranked as 'total-group Diplostraca' with a 'pre-clam shrimp' morphology, although eventually belonging to two different, not yet defined super-familial taxa. In addition, the 'primitive' nature of the posterior end of the body, with a multisegmented trunk and unspecified telson and furca, also suggests a primordial condition within the Diplostraca, and particularly distinguish both *Olesenocaris* and *Grauvogelocaris* from all Onychocaudata, which are (among additional features) characterized by articulated curved caudal furcae (Olesen & Richter 2013).

A superficially similar phyllopod was described as *Lioestheria monticula* Martens, 1983 from the lower Permian (Rotliegend) of Thuringia, Germany. It has a typical bivalve estheriid-type carapace with distinct coarse growth lines; if it were known only from the carapace it would have been assumed to be a fairly ordinary clam shrimp. However, a number of specimens possess an extended trunk composed of numerous subequal rings without appendages that extends beyond the carapace (Martens 1983, pl. 38, figs 1–3). *Lioestheria monticula*'s carapace superficially looks as though the margins could meet to fully enclose the animal (as in modern clam shrimp). Instead, its trunk would seem to prevent this from occurring.

Genus *Olesenocaris* nov.

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Derivation of name. Named after Jørgen Olesen (Copenhagen) for his contributions to understanding branchiopod phylogeny and biology; suffix from the ancient Greek καρίς, referring to shrimps and crayfish.

Type species. Olesenocaris galli from the Lower Triassic (upper Buntsandstein) Voltzia Sandstone Formation of the Vosges Mountains, France.

Diagnosis. Diplostracan genus with a laterally folded carapace, with barely curved posterior margin and with distinctly rounded posterolateral corners; trunk limbs well developed throughout, without marked morphological modification from the anterior part to the posterior end of the trunk; no disjunction in segmentation between dorsal segmentation of trunk and posterior limbs; abdomen multisegmented, devoid of appendages, composed of subcircular rings, extends from below the carapace for most of its length; telson with pair of caudal rami.

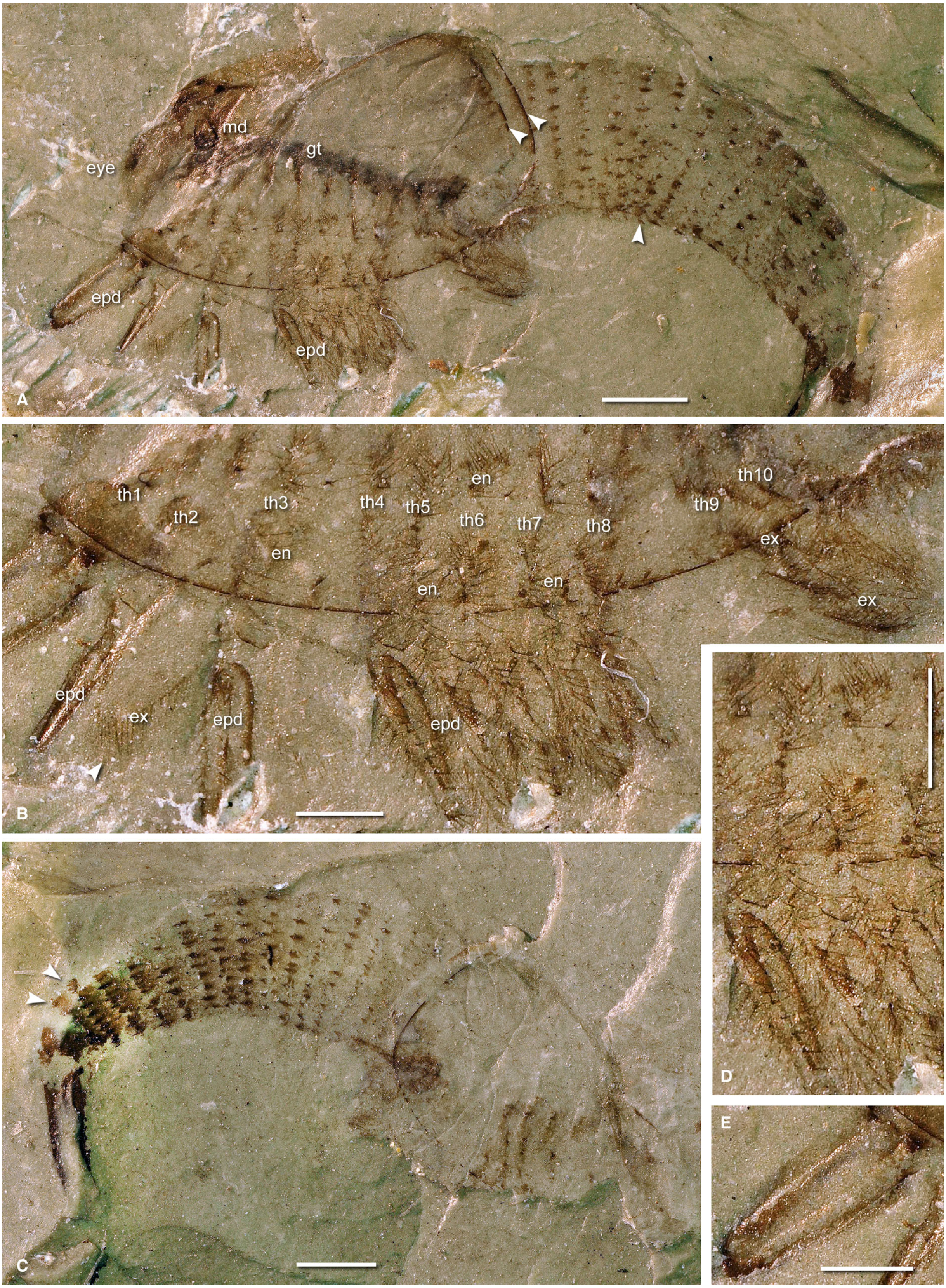
Remarks. Although the morphology is known only from only a single specimen, the new genus and species are clearly distinguished from the co-occurring calmanostracans by at least two striking differences of the carapace and the posture of the only known specimen. When allowed to decay in a calm environment, modern notostracans come to rest either dorsal side up or dorsal side down (TAH, pers. obs.) A lateral position is not stable; with a slight disturbance, the animal will topple over, although rare cases of laterally embedded crustaceans occur (e.g. Charbonnier *et al.* 2017). The position of this specimen from the Voltzia Sandstone suggests one of two different explanations: either the specimen was somehow supported in its lateral position (i.e. swept up in an obrution deposit), or it had a laterally compressed posture in life (similar to modern clam shrimp) that would allow it to come to rest on its side. Sedimentological evidence does not seem to support the former interpretation. Neither does a close examination of the morphology. The two posterior carapace corners of SMNS 75644-21a and b (Fig. 9A–C) are distinctly rounded, whereas the corners of *Apudites antiquus* are acutely pointed (e.g. Figs 2A, E, 4A, 5A–C). Unfolding the carapace of *Olesenocaris galli* would give a unique shape when compared with *Apudites antiquus* and other notostracan taxa.

In addition, the specimens exhibit additional striking differences in the appendages: SMNS 75644-21a and -21b do not have any small posterior limbs that decrease in size posteriorly and lose their correspondence to the regular dorsal segmentation. Every living notostracan, as well as most fossil notostracans (i.e. Gand *et al.* 1997, fig. 17A; Lagebro *et al.* 2015, fig. 2A) and kazacharthrans (McKenzie *et al.* 1991, fig. 3E) with well-preserved trunks show this feature. Exceptions are the early calmanostracans *Lynceites* Goldenberg, 1870 and *Heidiops* Werneburg & Schneider, 2023 (see below). This seems to be a possible synapomorphy of Calmanostraca + *Castracollis wilsonae* Fayers & Trewin, 2003 (Olesen 2009). The most similar fossil to this specimen is one identified by Ruedemann (1922) as *Apus beedei* (revision in progress by TAH) although reassigned to the genus *Triops* by Tasch (1969). Both of Ruedemann's specimens and the present specimens share the laterally folded carapace and the rounded posterior carapace corners.

Taken together in *Olesenocaris galli*, the laterally compressed carapace, curved posterior carapace corners, and lack of small posterior appendages are suggestive of a phylogenetic position close to the divergence of the Calmanostraca and Diplostraca. In addition, *O. galli* appears to lack well-developed feeler-like endites on the anterior thoracic appendages. Although the present specimens are imperfectly preserved in the region anterior to the first thoracic segment (Fig. 9A), it is highly improbable that an antennae-type limb was developed.

These differences in the morphology of the anterior thoracic segments clearly distinguish *Olesenocaris* from the co-occurring and superficially similar genus *Grauvogelocaris* (see below), which is characterized by an extended and branched second(?) antenna and does not show the distinctive structure that we identify as a complex eye or eye tubercle. The other differences include the shape of the carapace, which has a poorly curved posterior margin in *Olesenocaris* that contrasts with the gentle curvature of the posteroventral corner and the sharp posterodorsal edge of the carapace of *Grauvogelocaris*.

FIG. 9. *Olesenocaris galli* gen. et sp. nov. A–B, D–E, holotype, SMNS 75644-21a, nearly complete, laterally compressed specimen with largely preserved thoracopods: A, entire specimen showing mandible (md), dislocated gut track (gt), slightly different position of posterior rim of carapace (arrowed) and distinctly extended thorns on abdominal rings (arrow); note duplicated posterior margin of the carapace (arrows); B, magnified ventral region showing large terminal endopodites (epd; probably paired endopodites 5 and 6, partly with bristles), large bristles on endites (en), and smaller ones on probably partly preserved exopodites (ex); D, detail of mid-thoracic appendages showing arrangement of bristles; E, magnified view of large terminal endopodite at first thoracic segment. C, SMNS 75644-21b, counterpart of SMNS 75644-21a; nearly complete, laterally compressed specimen with remnants of limbs and differentially developed thorns on the abdominal rings (arrows). Scale bars represent: 1 mm (A, C) 500 μm (B, D, E).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Olesenocaris galli sp. nov.
Figure 9

? 1928 *Apudites antiquus* Schimper; Schmidt, p. 313, fig. 858 (lower left specimen only).
1971 *Triops cancriformis* (Schaef.); Gall, pl. 7.4 (only).
2006 *Triops cancriformis*; Gall *et al.*, p. 26 (specimen in lower right corner only).

LSID. https://zoobank.org/nomenclaturalActs/AE648A2B-C5CF-4CCF-817A-1EF7FF0119C8

Holotype. SMNS 75644-21a, b (= Ap5; part and counterpart). Only known specimens.

Type locality & type stratum. Philippe quarry near Vilsberg (WNW of Saverne; N 48°46′55″, E 7°14′45″); shales of the Grès à meules member of the Voltzia Sandstone Formation, upper Buntsandstein, lower Anisian, lower Triassic.

Derivation of name. Named after Jean-Claude Gall, in recognition of his contributions to the geology and palaeontology of the Voltzia Sandstone Formation.

Diagnosis. As for genus (by monotypy).

Description

General morphology. Dorsal carapace chitinous, slightly sclerotized, covering the cephalon and anterior part of the thorax, *c.* 43 mm long. Remaining part of the thorax and abdomen are well exposed. Number of anterior post-oral thoracopod-bearing thoracic segments probably 11. Boundary between thorax and abdomen difficult to determine, but anterior abdominal segments covered at posterior end of carapace. Abdominal section extended from carapace consists of *c.* 18–19 segments, terminating with a telson and probably a furca with two caudal rami. Total length of body from anterior margin of carapace to posterior tips of furca (in stretched-out condition) *c.* 11 mm; exposed trunk with furca 4.8 mm long, furcal rami *c.* 2 mm long.

Dorsal carapace. Dorsal carapace a laterally compressed or folded shield of roughly subelliptical outline (in lateral view); ventral margin gently curved, anteriorly grading into the weakly bowed dorsal edge with a relatively narrow curvature; posterior margin formed by a weakly curved edge grading into the dorsal and ventral margins with moderate curvatures. Apparent duplicated posterior margin in SMNS 75644-21a results from the preservation in which both valves are superimposed in slightly different positions (Fig. 9A, arrows). Surface of carapace smooth, margins without any spines, bristles or nodes. Maximum height of carapace *c.* 55% of maximum carapace length; maximum carapace length *c.* 45% of maximum body length (stretched out, excluding caudal rami). No details are recognized of any structures or organs expressed on the exterior of the carapace.

Cephalic & thoracic ventral anatomy. The subfrontal area of the dorsal carapace is imperfectly preserved, but appears to have been slightly more sclerotized. Vestiges of antennas are not recognizable and almost certainly were not significantly developed in *O. galli*. By contrast, the mandibular region is quite well visible and seems to be preserved in an almost 3D manner, in which a 'mandibular bulge' is seen in a squeezed obliquely lateral condition with a lobate middle portion connecting the paired mandibles in a yoke-shaped arc. The mandibles are seen as dark subelliptical areas connected indistinctly with the centrally located anterior part of the food groove and alimentary canal area, which extends posteriorly as a dark band (Fig. 9A, md, gt).

A singular structure is recognizable near the (not well preserved) anterior margin of the carapace. It is preserved as a dark, elliptical spot with delicate radial striae extending from it. We interpret the structure as a relic of a complex eye or eye tubercle. The imperfect preservation of the anterior margin of the carapace does not permit confident reconstruction of the morphology, but the course of the specimen's margin possibly indicates a slight modification in which the simply curved dorsoventral margin possibly has a small indentation, to allow complex eyes to extend from below the shield (Fig. 10), as seen in *Combinivalvula chengjiangensis* Hou, 1987 from the lower Cambrian Chengjiang Lagerstätte (see also Hou 1999).

The thorax is characterized by large thoracopods branched into well differentiated endites and with a sophisticated set of setae. It consists of 11 segments, with one pair of thoracopods at each segment. The first thoracopod is only slightly more extended than the following ones, but these limbs decrease only slightly in size rearwards.

A tentative reconstruction of the normal thoracic appendage is provided in Figure 11. However, the presence and location of adaxial endites is only suggested by concentration of dark organic matter and bristles. Each of these appendages consists of small endopodites and a larger exopodite. Protopodites are not recognizable with any certainty. In addition, no details of the morphology of the thoracopods can be identified with certainty, but vestiges of some of the exopods and endites together with remains of the setae are preserved in astounding detail. Long lamellae on the posterior margin of the exopodites and (less frequently) the endopods are sometimes preserved as a set of bristles (Fig. 9B–C). Particularly conspicuous are the distal ends of the thoracopods, which are interpreted as fairly massive pairs of endites. The first trunk limb, or thoracopod (th1) had slightly enlarged endopodites (Fig. 9E) but was otherwise not particularly extended by comparison with the following limbs (e.g. Fig. 9A–B).

The trunk limbs are generally similarly developed to those from *Apudites* and the triopsids, except for obviously less strongly developed gnathobases and exopodites. This suggests a food gathering method analogous to the modern triopsids, which feed on food particles from the detritus at the lake or pond bottoms. This appears to differ significantly from what can be concluded for *Grauvogelocaris* based on the development of the trunk limbs (see below).

The posterior part of the thorax is not recognizable with any confidence and (under consideration of its phylogenetic context) probably had simply developed limbs devoid of endites.

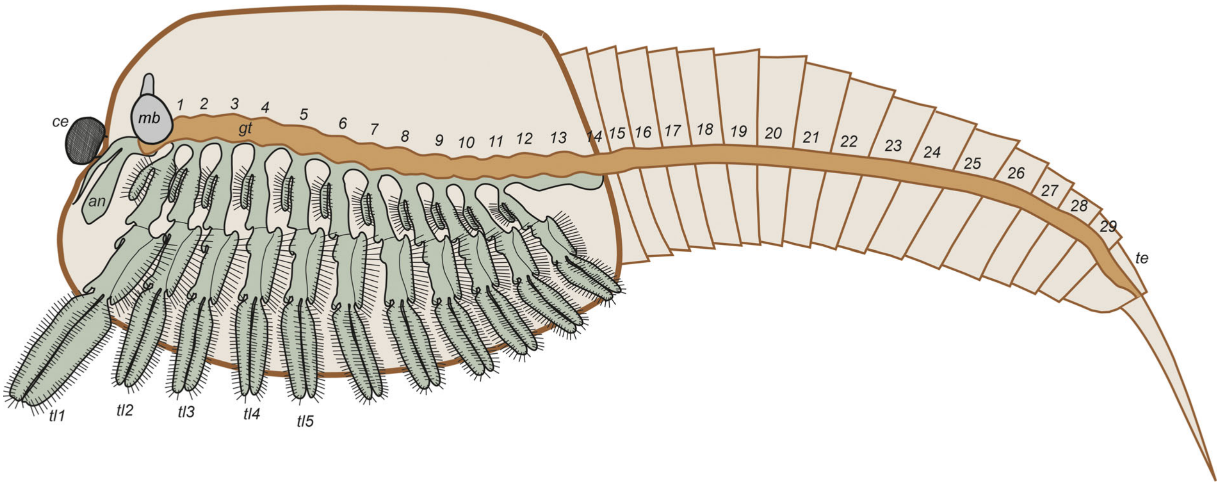


FIG. 10. *Olesenocaris galli*. Tentative reconstruction of the outlines of the carapace and trunk as well as ventral appendages. *Abbreviations*: an, antennal appendages; ce, compound eye; gt, gut track; mb, mandibular bulge; te, telson; tl1–5, trunk limbs 1–5; 1–29, somite number.

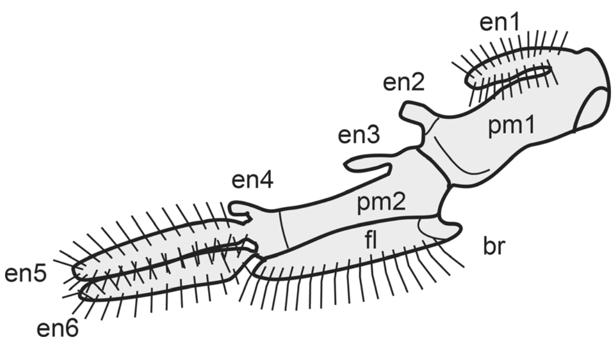


FIG. 11. *Olesenocaris galli*. Tentative reconstruction of anterior thoracopod. *Abbreviations*: br, weakly developed bract; en1–6, endites 1–6; fl, flabellum; pm1, pm2, podomeres.

Trunk/abdomen inclusive of telson. The abdomen consists of complete chitinous rings obviously without a central gap on the ventral side. A small foremost part of the thorax is covered by the carapace, but this part appears to include only two or three segments. The rings carry moderately large, sharp, rearwardly directed spines on their circumference at a subterminal position, creating a wreath-type crest on each of them. The spines or thorns vary slightly in size and extend somewhat beyond the posterior margin of the rings. The size of the trunk segments decreases successively in the rearward direction, creating a longitudinal conical outline. However, the decrease in diameter is minimal in the anterior half of the thorax and then progresses towards the posterior end.

The rear end of the trunk is imperfectly preserved in the Voltzia Sandstone material but ends in a ventrally curving telson with a pair of caudal rami of about half the abdominal length attached to it (Fig. 9C).

Digestive tract. The digestive tract is preserved as a dark, seemingly segmented strand. This 'segmentation' is regarded as a secondary phenomenon resulting from the imprint of the ventral limbs. The preservation is due to sediment filling starting around the oral opening near the mandibles. Remarkably, the dark staining ends abruptly near the posterior limbs.

Remarks. See above under genus.

Genus *Grauvogelocaris* nov.

LSID. https://zoobank.org/nomenclaturalActs/45260C2A-2D04-49AE-88A1-884A7979EF60

Derivation of name. Named after Louis Grauvogel (1902–1987), in recognition of his enormous contributions to the knowledge of the Grés de Voltzia Lagerstätte; suffix from the ancient Greek καρίς, referring to shrimps and crayfish.

Type species. Grauvogelocaris alsatica.

Diagnosis. Diplostracan genus with laterally folded carapace having gently curved posterolateral corners; trunk limbs well developed throughout, reduced in size and morphological development from the anterior part to the posterior end of the trunk; no distinct subdivision between limbs at anterior and posterior parts of the trunk; second antenna(?) extended, branched ('biramous'), distant segments form flagellum-like section; abdomen multisegmented, devoid of appendages, composed of subcircular rings, extending considerably beyond the carapace.

Remarks. Grauvogelocaris alsatica is a remarkable new genus and species of branchiopod, characterized by a bilobate, laterally compressed carapace that covers the entire trunk, whereas a large portion of the trunk extends rearward, its sag. length being nearly equal to that of the carapace and ending with a subcylindrical, obliquely truncated telson and probably paired furcal rami. The abdomen is relatively thick and consists of *c.* 16 spine-carrying ring-shaped exoskeletal units, devoid of any appendages.

The carapace has anterior and posterior margins slightly oblique to the axes, grading into the gently curved ventral margin via curved anteroventral and posteroventral corners, whereas the anterodorsal and posterodorsal corners are acute. The trunk limbs are well developed throughout. Their size decreases from the anterior part to the posterior end of the trunk. A distinct subdivision between limbs at the anterior and posterior parts of the trunk is not recognizable.

A particular development is recognizable for the presumed second antennae: it extends ventrally clearly beyond the margin of the carapace. At least three distinct flagella are visible, although this may be due to overlaying of the flagella of left and right limbs (Fig. 12A).

This morphology of a bivalved carapace without distinct organs recognizable on the exterior of the carapace, a gradient in size and morphology of the trunk appendages devoid of phyllopods, and the abdomen composed of sub-cylindrical exoskeletal rings without any appendages, clearly suggests that *Grauvogelocaris* is a diplostracan. Although the carapace superficially resembles some spinicaudatan genera in shape, it appears to lack the growth lines caused by moult retention. The trunk, which distinctly extends from the carapace, distinguishes the genus and species from all living spinicaudatans. As above, *Lioestheria monticula* is an important comparison to bear in mind. Given that the soft parts are known from only a small percentage of the 'conchostracans' it cannot be ruled out that similar forms have been discovered, but unrecognized because their identification was based solely on fossilized carapaces. However, the morphology presented by *Grauvogelocaris* suggests that it represents a stem lineage diplostracan, formally attributable only to a hitherto unknown suborder.

For differences to the co-occurring *Olesenocaris* see the discussion under that genus (above).

Grauvogelocaris alsatica sp. nov.
Figure 12A–B,? C

LSID. https://zoobank.org/nomenclaturalActs/3798FF7A-5C61-4335-8BC1-27D550A87E94

Derivation of name. From *Alsatia*, Latin word for the French region Alsace; a reference to the region in eastern France, from which the specimens were collected.

Holotype. Specimen SMNS 75644-6a (Fig. 12A–B).

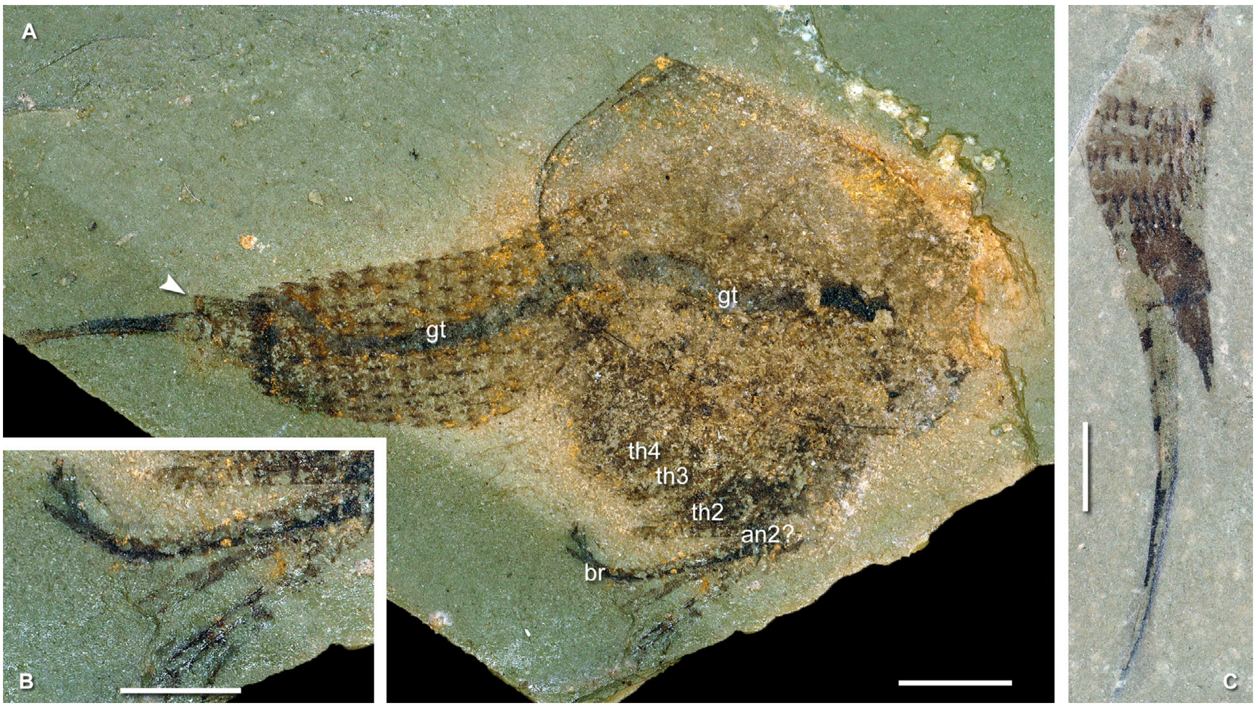
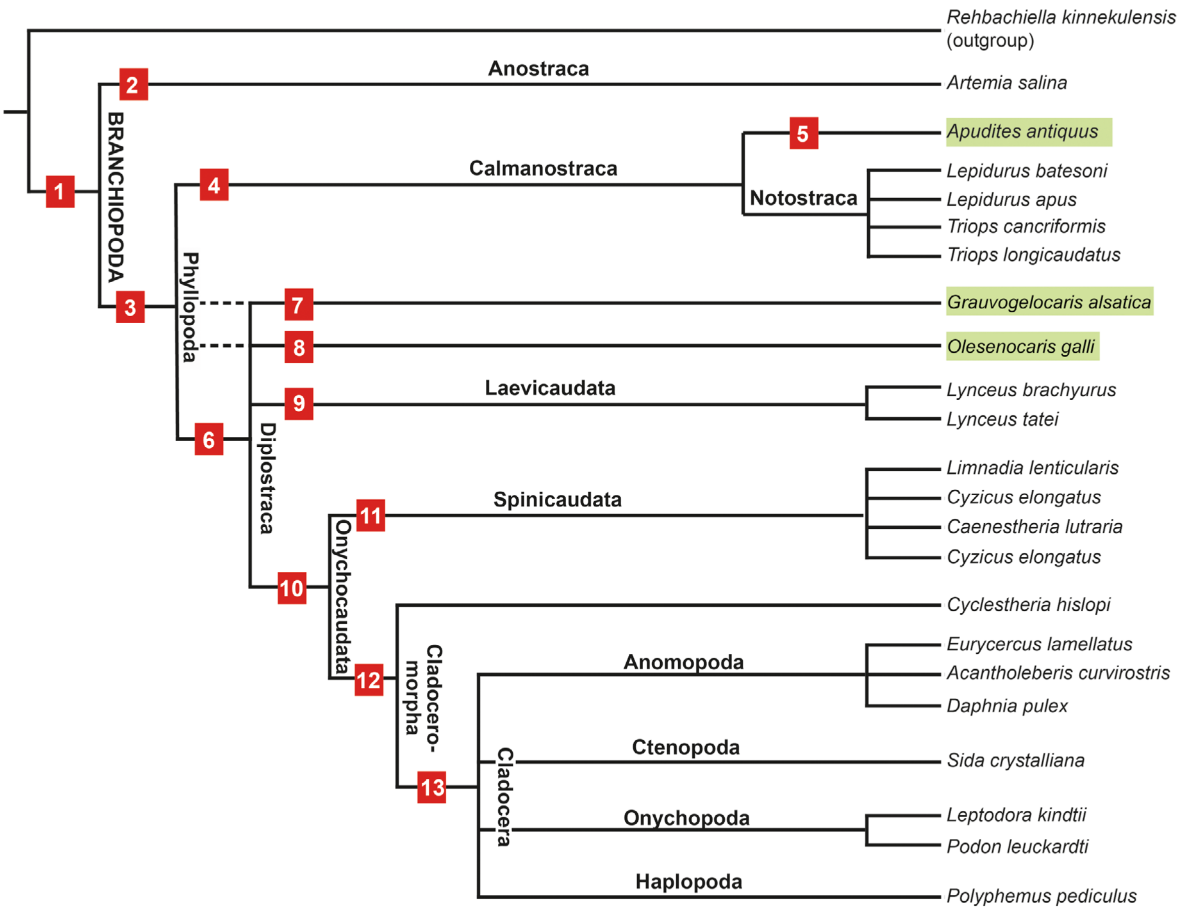


FIG. 12. A–B, *Grauvogelocaris alsatica* gen. et sp. nov., holotype, SMNS 75644-6a, nearly complete, laterally compressed specimen with thoracopods (th) preserved as dark, somewhat blurry masses ventrally extending beyond margin of carapace; note obliquely truncated telson (arrow): A, entire specimen, black curved gut track (gt); telson shows sigmoidal curvature of posterolateral margin and sharp dorsal edge (arrow); note extremely large extensions of second antenna(?) (an2?); B, magnification of second antenna(?). C, SMNS 75644-19b; specimen tentatively assigned to *Grauvogelocaris alsatica*; partial trunk and subrectangular telson (note slightly concave lateral margins) with attached caudal rami, which are almost in contact on the median line. Scale bars represent: 1 mm (A, C); 500 μm (B).



Node	Taxa	Synapomorphies
1	Branchiopoda	• Mandibular gnathal edge consists of large ellipsoid molar process • Maxilla 1 and maxilla 2 reduced • 11 pairs of trunk limbs; six endites on trunk limbs • Trunk limbs with unsegmented endopod
2	Anostraca	• Carapace absent • Pedunculate eyes • Ventral brood pouch
3	Phyllopoda	• Pair of setae on the telson • Internalized compound eyes • Trunk limbs with 5 endites
4	Calmanostraca	• Carapace developed as a flattened dorsal shield • Second antennae uniramous and unsegmented • Trunk limbs subdivided into sclerotised sections • Posterior limbs lose the 1:1 correspondence to dorsal segments
5	*Apudites*	• Endopodite on first thoracic appendages matches the morphology of succeeding thoracic limbs • Shield-shaped, flattened dorsal carapace
6	Diplostraca	• Biramous second antennae • All trunk segments with limbs • Carapace laterally compressed, covers limbs and head • Trunk limbs with long dorsal extension of exopod • First pair of thoracic limbs claspers (in males)
7	*Grauvogelocaris*	• Second antenna extended and biramous (synapomorphy with Diplostraca?) • Posterior part of trunk extending beyond carapace, with sclerotised integument with subcircular cross-section (synapomorphy with Calmanostraca?)
8	*Olesenocaris*	• Laterally folded carapace with rounded posterior corners (synapomorphy with Diplostraca?) • Endopodite on first thoracic appendages matches the morphology of succeeding thoracic limbs • Trunk with 10(?) appendages, posterior part extending beyond carapace, with sclerotised integument with subcircular cross-section (synapomorphy with Calmanostraca?)
9	Laevicaudata	• Thorax consisting of 10–12 segments • Abdomen reduced to a single anal somite
10	Onychocaudata	• Carapace with growth lines (lost in Cladocera) • Trunk limbs used for feeding only • Telson laterally compressed, with spines arranged in two rows • Furcae curved and claw-like • Ommatidial part of compound eyes fused to a globular organ
11	Spinicaudata	• Second pair of trunk limbs developed as claspers in males
12	Cladoceromorpha	• First antennae sensilla restricted to tip • Heterogony (alternation between sexual and asexual reproduction)
13	Cladocera	• Carapace covers limbs, head is free • Adult second antennae with four segments in exopods and four segments in endopods • Six pairs of trunk limbs • Dorsal extension of trunk limb exopods lost • Embryos carried under carapace with no connection to exopods

FIG. 13. Phylogenetic tree (modified from Hegna 2012) of the proposed systematic relationships among the Branchiopoda, showing the positions of *Apudites antiquus*, *Olesenocaris galli* and *Grauvogelocaris alsatica*. Numbers refer to the characters listed below the tree.

Material. The only unequivocal specimen assigned to *Grauvogelocaris alsatica* is the holotype (SMNS 75644-6a) and its counterpart (SMNS 75644-6b). A second, unregistered specimen from the Grauvogel collection appears to represent the same species but is too poorly preserved to enable recognition of any details. A partial trunk with attached telson and furca (SMNS 75644-19b, Fig. 12C) is tentatively assigned to the species.

Type locality & type stratum. Philippe quarry near Vilsberg (WNW of Saverne; N 48°46′55″, E 7°14′45″); shales of the Grès à meules member of the Voltzia Sandstone Formation, upper Buntsandstein, lower Anisian, lower Triassic.

Diagnosis. Diagnosis of genus (because of monotypy).

Description. Grauvogelocaris alsatica has a bivalved carapace covering the entire trunk. Carapace with obliquely subrhomboidal outline, anterior and posterior margins slightly oblique to axes, grading into a gently curved ventral margin. Anteroventral and posteroventral corners broadly curved; anterodorsal and posterodorsal corners acute, both enclosing an obtuse angle. The holotype had a maximum length (from anterior margin of carapace to posterior tips of furca) of *c.* 9.5 mm.

The trunk limbs are imperfectly preserved and recognizable in the specimen, but were well developed throughout. Size of limbs decreases from the anterior part to the posterior end of the trunk, and their morphological development appears to be less diversified as well. An extended limb that stretches conspicuously ventrally beyond the margin of the carapace most probably represents the second antenna; it is branched into apparently at least three distinct rami, distant segments form a flagellum-like section, but with a brush-like tip (Fig. 12A–B). The preservation of the thoracopods suggests that they were setous, but further details about the limbs are not easily interpreted. A distinct subdivision between limbs at anterior and posterior parts of the trunk is not recognizable. Thoracopod 2(?) is slightly more elaborately developed than the thoracic limbs posterior to it and can be seen partially preserved in SMNS 75644-6a. The remainder of the thoracic appendages continuously decrease in size and have less pronounced distal parts, but do not show a distinctive subdivision into well-developed thoracopods in the anterior part of the trunk and reduced limbs in the posterior trunk (Fig. 12A).

The large trunk extends rearward, its sagittal length nearly equal to that of the carapace; relatively thick, consists of *c.* 16 subcylindrical exoskeletal units of (apparently) subcircular transverse section, devoid of any appendages. The rings, however, have a wreath of relatively large subterminal thorns separated by slightly varying distances (*c.* 25 per ring).

The trunk terminates in a subcylindrical telson, which is obliquely truncated in lateral view (Fig. 12A, arrow), with probably paired furcal rami attached to it. Notably, the furcae insert well below the dorsal side of the telson. The posterior edge of the dorsal side, which hangs above the furcae, may be homologous with the spiniform projection that is well developed above the cercopods (= furcae) in modern spinicaudatans.

Remarks. The trunk limbs provide clues to the functional morphology. They obviously formed a capture device that (analogous to similar arthropod appendage combination) may have acted in a synchronized order for gathering food. In this case, the food particles were more likely to have been captured from the water rather than from the detritus on the bottom of the lakes or ponds as in notostracans or *Olesenocaris*. Remarkably, the digestive tract in *Grauvogelocaris* is preserved as a blackish stained and winding band without a 3D aspect, which perhaps indicates the absence of sediment particles that are in turn indicated by massive, 3D tubes in some specimens of *Apudites antiquus*. The trunk segmentation is partly imprinted upon the digestive tract.

The telson of *Grauvogelocaris alsatica* is not known from a well-preserved specimen that shows a dorsal aspect. Although preserved only laterally compressed, the relationship to the posterior trunk segments suggests that the telson was generally less voluminous than the posterior thoracic segments. It most probably had a subquadrate to subrectangular outline with a slight convex curvature of the posterior margin. It appears to indicate a slight change in the diameter between the midgut and the hindgut. The dark tint of the digestive tract indicates that the anus is located near the end of the telson.

SYSTEMATIC RELATIONSHIPS OF THE VOLTZIA SANDSTONE BRANCHIOPODS

The systematic position of the three branchiopods from the Voltzia Sandstone Lagerstätte can be plotted into a phylogenetic tree with a relatively high amount of certainty. Such phylogenetic trees of the supposed systematic relationships among the Branchiopoda have been presented in numerous studies (e.g. Olesen 1998, 2009; Richter *et al.* 2007). A comprehensive study by Hegna (2012) presented an integrative approach that led to alternative consensus trees. In fact, Hegna (2012) included the taxa studied herein, albeit with unofficial manuscript names.

Using these results, we illustrate a phylogenetic tree derived from Hegna (2012) based on cladistic analyses conducted under different parameters and denote supporting synapomorphies (Fig. 13). In respect to the branchiopods from the Voltzia Sandstone Formation, these characters have been discussed above under the relevant taxa.

Particular emphasis needs to be placed on the fact that the position of *Apudites* according to the discussed characters does not necessarily indicate that *Apudites* is a member of the Notostraca as presently defined. However, this fact results from the deficiency of characters identified from fossils and a rather limited plasticity of morphological characters in extant notostracans.

CONCLUSIONS

1. Careful re-study of the notostracans from the Lower Triassic Voltzia Sandstone Formation of Alsace

indicates that these are distinct from the Recent species *Triops cancriformis* and cannot even be assigned to the family Triopsidae.
2. The originally applied genus and species names, *Apudites antiquus*, are available and appropriate for them.
3. All well-preserved pre-Cretaceous notostracan fossils studied thus far appear to represent non-triopsid calmanostracan taxa.
4. A few specimens from the Voltzia Sandstone Formation that have been previously assigned to *Triops cancriformis* as well, represent genera and species with a laterally compressed, bivalved/bilobate carapace and are stem-lineage members of the Diplostraca or 'total-group Diplostraca', which are introduced as *Olesenocaris galli* gen. et sp. nov. and *Grauvogelocaris alsatica* gen. et sp. nov., respectively.
5. *Olesenocaris galli* and *Grauvogelocaris alsatica* differ considerably in their ventral anatomy and are not closely related. In addition, the differences between their appendages suggest potentially different modes of food gathering.
6. Preservation of some specimens of *Apudites antiquus* as well as *Olesenocaris galli* and *Grauvogelocaris alsatica* offers morphological details in a way that ranks them among the best-preserved fossil non-marine arthropods.
7. All three species provide or lack characters that enable them to be readily placed among the existing relevant suprageneric taxa.
8. A phylogenetic tree of the supposed systematic relationships among the Branchiopoda, and which suggests the position of *Apudites antiquus*, *Olesenocaris galli* and *Grauvogelocaris alsatica*, is shown in Figure 13.

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Author contributions. **Conceptualization** G Geyer (GG), TA Hegna (TAH); **Formal Analysis** GG, TAH; **Investigation** GG, TAH; **Methodology** GG; TAH, K-P Kelber (KPK); **Resources** GG, TAH; **Software** GG; KPK; **Supervision** GG; **Writing – Original Draft Preparation** GG, TAH, KPK; **Writing – Review & Editing** GG, TAH, KPK.

DATA ARCHIVING STATEMENT

This published work, and the nomenclatural acts it contains, have been registered in ZooBank: https://zoobank.org/references/D39C9A9D-D2B3-4986-998A-6589B3532C5E.

Editor. Arnaud Brayard

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