

## NEW TRIASSIC ASTEROIDEA (ECHINODERMATA) SPECIMENS AND THEIR EVOLUTIONARY SIGNIFICANCE

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**Abstract.** The Paleozoic-Mesozoic transition saw the disappearance of asteroid stem groups and the ascent of the crown group, but late Paleozoic and Triassic asteroids are rare and transition events are poorly documented. Three new Middle and Late Triassic specimens augment existing data; included are a specimen of *Trichasteropsis weissmanni* from Germany, a specimen of *Trichasteropsis?* sp. indet. from Italy, and a possible member of the extant Poraniidae from Slovenia. Presence of a small ossicle at the interbrachial midline and adjacent to the marginal series of the new *T. weissmanni* specimen is consistent with similar expressions not only of other trichasteropsids but also occurrence of two interbrachial ossicles in Paleozoic, stem-group asterozoans; presence is in turn consistent with a hypothesis of derivation of the axillary/odontophore coupling from two ossicles rather than direct derivation of the crown-group odontophore from a single stem-group axillary. Morphology of *Trichasteropsis?* sp. indet., including, for example, the evenly-tapering arms are reminiscent of those of diverse crown-group asteroids whereas the enlarged distal arms of *T. weissmanni* are unique, the morphology of *T?* sp. indet. thereby potentially indicative of a plesiomorphic, stemward positioning within the Trichasteropsiidae. The range of the Poraniidae is tentatively extended to the Carnian. Similarities shared by the Poraniidae and the Trichasteropsiidae suggest stemward positioning within crown-group diversification; however, known Triassic fossils do not appear closely related to extant taxa identified in recent molecular studies as basal within the crown-group. A temperate climate is suggested as preferred by the Triassic asteroids rather than a tropical, warmer one.

## INTRODUCTION

Studies of fossil asteroids traditionally assigned the earliest (Ordovician) body fossils to crown-group ordinal-level taxa, with few families thought to have survived the Paleozoic-Mesozoic transition (Ubaghs 1953; Spencer & Wright 1966); more recently, differences between faunas of the eras have received even greater emphasis (Blake 1987; Gale 1987, 2011, 2013; Blake & Mah 2014). Morphologic data bearing on the origin of the crown group from both modern taxa and the very limited fossil record nevertheless are ambiguous; however, consensus on the basal crown-group asteroid as based on molecular analyses appears to be emerging (Janies 2001; Janies et al. 2011; Mah 2006, 2007; Mah & Foltz 2011a, 2011b, 2014; Pisani et al. 2012; Telford et al. 2014; Feuda & Smith 2015).

Many factors potentially contributed to the scant asteroid record through the Paleozoic-Mesozoic interval. The comparatively delicate, articulated construction of asteroids does not lend itself to ready preservation, and asteroids of all ages are rare at almost all localities. Late Paleozoic and early Mesozoic taxonomic diversity might have been limited, or only few asteroids might have been present in environments most readily incorporated into the relatively modest stratigraphic record of that interval. There are taxonomic uncertainties as well; although Triassic diversity is limited, diverse modern faunas can be dominated by relatively few species (e.g., Walenkamp 1976, 1979), and perhaps ancient faunas now represented by only few taxa could have been more diverse, as is suggested by the Early Devonian Hunsrück Slate (Lehmann 1957) for that particular geologic interval. Sampling of the fossil record will emphasize numerical dominants from favored environments, although these dominants might be distant from clade diversification, and therefore misleading as phylogenetic

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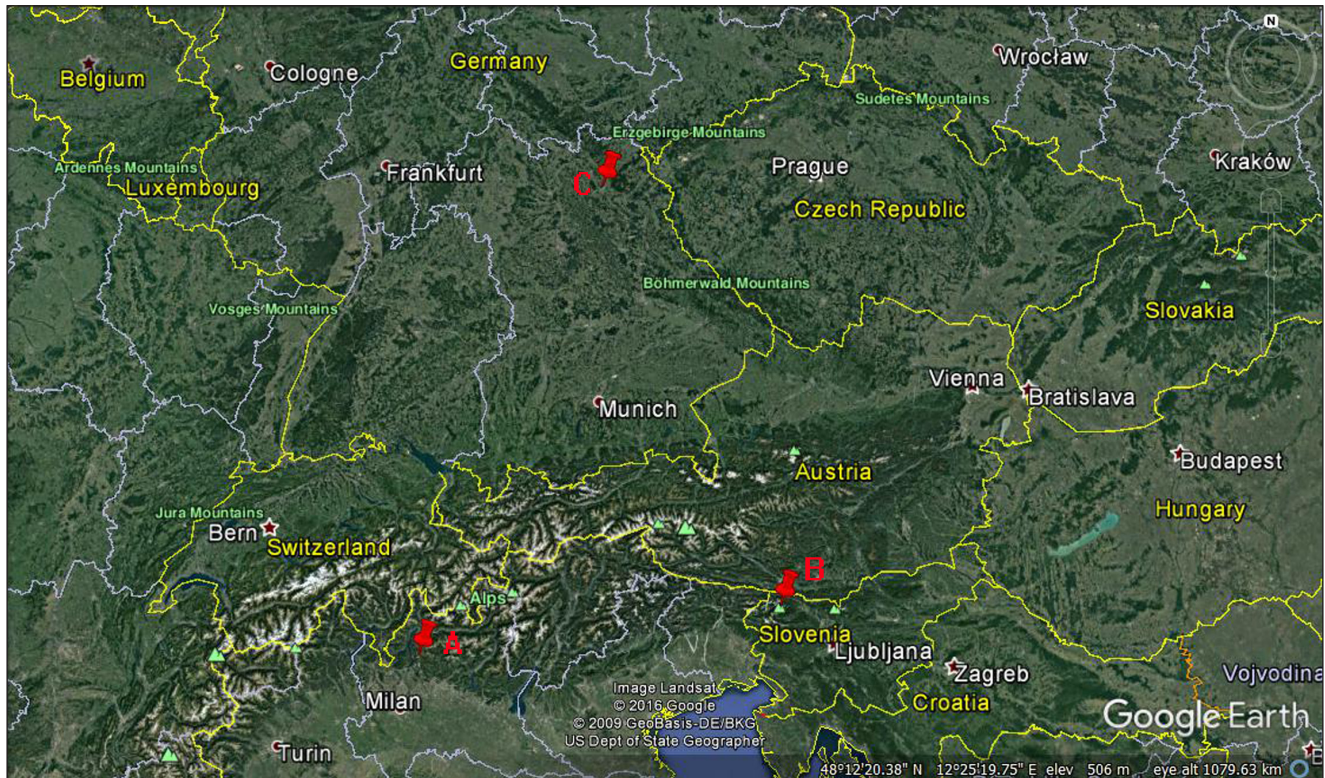


Fig. 1 - Geographical maps for the find sites. A, the Northern Grigna (Lecco, Italy); B, Vrata Valley (Triglav Mountain, Slovenia); C, Bindlach, (Bayreuth, Germany).

indicators. Assessment of Triassic fossils demands interpretation of species, generic, and familial concepts, yet the Triassic might have been a time of ecological conditions and evolutionary demands different from those leading to emergence of extant species; interpretation of taxon boundaries across large intervals of time and potentially significant environmental change is problematic (Blake et al. 2015).

Three new specimens from the European sequences (Figs 1, 2) that have provided the bulk of described Triassic asteroids are discussed (Pls 1, 2). Faunal associates and geological data indicate normal marine settings for all. Taxon affinities appear close to those of previously described Triassic occurrences.

## TERMINOLOGY

Primary ossicles form the foundation framework of asteroids. Accessory granules, spines, and pedicellariae attach to primaries. Paired ambulacral ossicles form the vaulted ambulacral furrow, and they abut the ventrally placed adambulacrals. Marginal ossicles, developed in one or two series (“superomarginals” and “inferomarginals”), form the ambital edge.

Abactinal ossicles are dorsal to the marginals, and actinal ossicles lie between the marginals and adambulacrals. Orientation terminology for individual ossicles parallels that for intact specimens. Proximal is toward the vertical (dorsal-ventral) axis centered on the mouth and distal is away from this axis. Adradial is toward the arm midline and abradial is away from the midline. Length is parallel to the arm midline and width is perpendicular to the midline; ossicles therefore can be “wider” than “long.” Height is the third dimension, perpendicular to length and width; ossicles can be described as “low” or “high.” Spencer & Wright (1966) provided more extended treatment of terminology.

## ON THE PHYLOGENY OF THE CROWN-GROUP ASTEROIDEA

A comprehensive history of asterozoan classification was provided by Spencer & Wright (1966, p. 35); this information is not repeated here. Early researchers on extant asteroids emphasized morphologically-based taxonomy; attempts to evaluate any phylogenetic perspectives of these authors is proble-



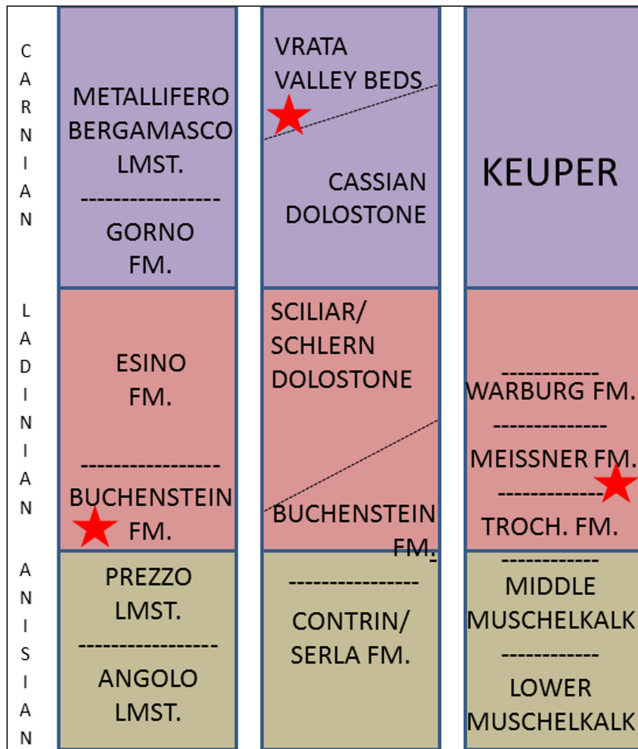


Fig. 2 - Stratigraphic position of the described specimens. A, the Northern Grigna (Lecco, Italy); B, Vrata Valley (Triglav Mountain, Slovenia); C, Bindlach, (Bayreuth, Germany). The red stars indicated the position of the described specimens in the local stratigraphic series.

matic, in part because earlier treatments can suggest phylogenetic interpretation to the contemporary reader where none might have been intended. Taxon arrangements in monographs provide exemplification: taxa must be ordered in any publication, and phylogenetic implications should not be read into any selected sequencing (A.M. Clark, pers. comm. 1983).

Interpretation of the evolutionary history of extant asteroidea has been contentious. Phylogenetic relationships were first extensively debated by Th. Mortensen and E.W. MacBride in the pages of *Nature* during the early 20th century, the debate reviewed by Blake & Mah (2014). Mortensen posited the Astropectinidae as basal among extant asteroidea based in part on an apparent lack of a brachiolarian larval stage as well as absence of suckered tube feet whereas MacBride argued these absences were secondary, resulting from occurrence on shallow, unconsolidated substrates; a basal taxon was not offered by the latter author. Subsequently, Fell (e.g., 1963) indirectly supported argumentation of Mortensen in placing the astropectinid-like Luidiidae at the base of asteroidea diversification.

Earlier summaries by paleontologists projected diversification of the extant, approximately ordinal-level clades during the Ordovician (e.g., Spencer & Wright 1966, see fig. 38) whereas more recently, authors have favored emergence of the crown-group during the later Paleozoic to early Mesozoic interval (Gale 1987, 2011, 2013, 2015; Blake 1987; Mah & Blake 2012; Blake & Mah 2014). The later authors have broadly agreed on timing of crown-group diversification and much important taxon configuration; however, recognition of the basal crown-group as based on morphologic criteria is problematic in part because the few available late Paleozoic stem-group fossils allow development of divergent viewpoints, Gale favoring a basal positioning for the Paxillosida, including the Astropectinidae, and Blake favoring a dichotomy separating the forcipulatacean asteroidea from the remainder, including the Paxillosida.

Molecular analyses beginning during the later 20th century have led to dramatic rearrangements of phylogenetic interpretations of many invertebrate taxa, including that of asteroidea (Janies et al. 2011; Mah & Foltz 2011a, 2011b; Feuda & Smith 2015). A result important to the search for the Paleozoic source (or sources) of the crown group, and not predicted from earlier morphologic work, is the emergence in molecular treatments of the atypical Pterasteridae in a stemward position (Janies et al. 2011; Feuda & Smith 2015). At present, it appears likely that evolving molecular techniques will ultimately prove fundamental to the basic taxonomic arrangement of crown-group asteroidea, although paleontologists will continue to search for potential sources among Paleozoic asteroidea, and morphology and other researches (e.g., developmental biology) certainly will continue important to the interpretation of other aspects of asteroidea biology, such as functional morphology and ecology.

## THE AXILLARY AND THE ODONTOPHORE

An ossicular expression potentially useful to the interpretation of crown-group derivation is the relationship between the so-called axillary and odontophore. Among Paleozoic representatives, the axillary traditionally was envisioned as an unpaired, interbrachial, external ossicle aligned with the marginal series, and at least in most species, abutting

the MAO pair; among species with many actinal ossicles and enlarged disks, the axillary can be difficult to recognize. Among most crown-group asteroids, the odontophore is fully internal, interbrachial, and immediately dorsal to the MAO; axillaries, in the traditional sense, have not been recognized in the crown group. Spencer (1916, p. 62) was of the view that the axillary, which is very prominent for example in the Hudsonasteridae (Spencer & Wright 1966, fig. 47), became the internal odontophore of crown group usage, a perspective retained in Spencer & Wright (1966, p. U29); these authors derived their axillary/odontophore ultimately from the inframarginal (=inferomarginal) series (p. U14). In illustrating and discussing a number of ancient and extant asteroids, Gale (2015) was consistent with the views of Spencer (1916) in proposing a phylogenetic transformation leading from the stem-group axillary to the crown-group odontophore.

A second hypothesis consistent with the Spencer and Wright derivation of the odontophore ultimately from an inferomarginal is the potential derivation of the axillary/odontophore not from one but from two ossicles. Both an enlarged external axillary and a tiny internal ossicle behind the MAO pair occur in *Hudsonaster narrawayi* (Hudson, 1912; pl. 1, 3), the specimen re-illustrated by Schuchert (1915, pl. 1), who also correctly identified the vaulted ambulacral ossicles of the arm interior that had been previously judged by Hudson to be external, ambulacral cover plates. Hudson's specimen appears to have been the basis for the reconstruction of Kesling (1962, fig. 2; reproduced by Spencer & Wright 1966, fig. 47.3c) under the name *Protopalaeaster*, Kesling reinterpreting the Hudson photographs to represent an external appearance but incorrectly retaining the tiny internal ossicle in this reconstruction. Additionally, two ossicles occur at the interbrachial midline of the stenuroid *Embolaster* (Blake 2008), Branstrator (1975, p. 179, 186) recognized both an unpaired inferomarginal axillary and a V-shaped "true odontophore" in the Promopalaeasteridae, and a V-shaped internal ossicle occurs in *Jugiaster* (Blake 2007, fig. 2.1, 2.2). Finally, Gale (2015, fig. 1G) blue-highlighted an unpaired ossicle interpreted as an inferomarginal immediately distal to the green-highlighted inferred odontophore of the Permian asteroid *Monaster clarkei*, the ossicular pair here considered likely homologues of the pairing of the other genera cited above; that is,

the alternative hypothesis to that of Spencer (1916) and Gale (2015) is that the internal odontophore of the crown group together with the external axillary have always been separate ossicles, and both were in place from early in asterozoan history.

## IMPLICATIONS OF THE ORDER TRICHASTEROPSEIDAE

A hypothesis of two ossicles raises the question, what happened to the more lateral, traditional "axillary"? Ultimately, the best answers likely need to be sought in developmental biology through tracking the formation of the skeleton during early ontogeny, but Triassic trichasteropsids, representing the crown group (Blake & Hagdorn 2003; Gale 2011) nevertheless provide pertinent data.

Presence of an unpaired ossicle at the edge of the disk and bordering the marginal series on the interbrachial midline of small specimens of the then-new trichasteropsid genus *Migmaster* (Blake et al. 2006, fig. 3D, 3E) raised the possibility that this ossicle represents the second "axillary" ossicle. Gale (2011, p. 65) rejected the posited homology, arguing that the edge ossicle cannot be an axillary equivalent because it does not articulate with the mouth-angle pair, the argument apparently based on assumption of presence of only a single axillary/odontophore ossicle, which is countered by presence of two ossicles in multiple Paleozoic occurrences; it further assumes that a single ossicle could not be displaced from the mouth-angle pair. The described new *T. weissmanni* specimen has a comparable, small, unpaired ossicle essentially at the interbrachial midline and at the marginal frame of all five interareas (Pl. 2, fig. 2, 3); a corresponding ossicle in other trichasteropsid specimens (Blake & Hagdorn 2003, fig. 2E; Blake et al. 2006, fig. 3D, 3E) establishes that presence in the new specimen is more than an individual peculiarity. Further, positioning and to some extent form in the trichasteropsids is comparable to the blue-highlighted "inferomarginal" of Gale (2015, fig. 1G) of stem-group Permian *Monaster*. Presence does not prove that the ossicle of trichasteropsids is the second axillary homologous with the enlarged external axillary of e.g., hudsonasterids, but argumentation is needed for such a hypothesis to be rejected. Unfortunately, observations on the interior of the mouth frame of trichasteropsids are not yet

available, and differing interpretations are possible whether the internal ossicle proves to be present or not; for example, an internal odontophore would support the two-ossicle hypothesis and historical continuity whereas its absence would at least favor placement of pertinent species away from the mainline of crown-group evolution.

The unpaired, interbrachial ossicle of trichasteropsids is very small, at least in larger specimens, although proportionately large in small *Migmaster*, Blake et al. (2006, fig. 3D, 3E). The actinal field of most crown-group asteroids contains many ossicles, the once-important axillary potentially remaining unidentified, reduced, and obscured, thereby documenting a need for study of early skeletal ontogeny among extant exemplars.

#### ASPECTS OF THE FOSSIL RECORD OF THE TRIASSIC ASTEROIDEA

Described Triassic asteroids are comparatively few, and although authors agree that all can be assigned to the crown group, specific affinities within the crown group have been tendentious (e.g., Blake 2003; Gale 2011). Interpretation of Triassic asteroid affinities is important to the interpretation of the Paleozoic to Mesozoic transition as well as to the transition to the younger asteroid faunas, all members of which have been more or less closely aligned with extant orders and families.

The order Trichasteropsida Blake & Hagdorn, 2003, although limited to Triassic occurrences, was assigned to the surviving Forcipulatacea (Blake 1987; Blake & Hagdorn 2003, including phylogenetic analysis; Blake et al. 2006; Mah & Foltz 2011; Mah & Blake 2012; Blake & Mah 2014). There are uncertainties, which led to a section “A clouded look at the base of the crown group” (Blake & Hagdorn 2003, p. 30); an important uncertainty is that pedicellariae have not been recognized in the Trichasteropsida, although they are abundant and varied among extant forcipulataceans. As relatively well preserved as the new *T. weissmanni* specimen is, no pedicellariae can be recognized; however, because forcipulatacean pedicellariae are unlike those of other extant asteroids, it is possible that they arose within forcipulataceans only after the trichasteropsid grade of evolution.

Alternative viewpoints on the affinities of *Trichasteropsis* have been published: Spencer & Wright (1966), in the influential *Treatise on Invertebrate Paleontology*, minimized generic significance in aligning *Trichasteropsis* with the Paleozoic genera *Palasterina* McCoy and *Palaeosolaster* Stürtz in the family Palasterinidae. Gale (2011, p. 63 et seq.; 2013) challenged interpretations of Triassic asteroids of Blake & Hagdorn (2003) and Blake et al. (2006), including the new genus *Migmaster*, in part summarizing divergent earlier assignments of *Trichasteropsis* and in part arguing that many morphologic expressions of these genera are to be found elsewhere in the crown group. Blake & Mah (2014) responded and retained earlier perspectives, which are retained here as well.

Complimenting the similarities between *T. weissmanni* and extant forcipulataceans described in earlier papers, morphology of the new *T. weissmanni* is posited as consistent with phylogenetic linkages between trichasteropsids and many extant forcipulataceans, and therefore certain expressions in later forcipulataceans are potentially plesiomorphic. Other expressions, however, are either distinctive or incompletely known; for example, the mouth frame of the new *Trichasteropsis* (Pl. 1, fig. 8, 9) appears distinct from those documented for extant asteroids (e.g., Gale 2011), calling for ongoing research with this and other trichasteropsid material.

In an extended study, Gale (2011) carefully documented much asteroid ossicular detail, including that of the mouth angle ossicles, for a suite of genera representing taxonomically diverse extant families. No attempt is made here to apply this author’s detailed terminology because time of occurrence between Triassic and living asteroids together with taxonomic disparity between extinct Trichasteropsida and the documented extant forcipulataceans of Gale would render any attempt at precise comparison troubling; beginning with the present forcipulatacean interpretation of trichasteropsids, the significant variation among mouth-angle ossicles in the extant forcipulatacean sampling argues any specific attempt at precise comparison would claim unintended certainty of details. Alignment of trichasteropsids with forcipulataceans (Blake & Hagdorn 2003) is based on many aspects of body wall and ambulacral expression but not on precise expressions of the mouth-frame ossicles. It is not argued here that details of mouth frame configuration at present contribute significantly to under-



standing of taxon affinities, in part because what can be seen of mouth ossicles of the new *T. weissmanni* appear apart from those of extant forcipulataceans.

The outer faces of the upright mouth angle ossicles (MAO) of *T. weissmanni* are small (Pl. 1, fig. 8, 9), although the MAO are high, somewhat thickened, and enlarged dorsally relative to expressions typical of the extant forcipulates. Multiple adambulacrals of adjacent furrows of many extant forcipulataceans abut behind the mouth angle ossicular pair to form an “adoral carina”; only one or two adambulacrals abut in *T. weissmanni* (Pl. 2, fig. 2, 3). The circumoral of *T. weissmanni* is peculiar in that it is enlarged and of an overall “J”-shape with both arms of “J” articulated with the MAO, and an unclosed podial receptor facing the mouth (Pl. 1, fig. 8, 9).

Specifics of ventral disk configuration, including of the mouth frame, accompanied differentiation of a conical depression surrounding the mouth area, the so-called “actinostome,” which in *Trichasteropsis* is similar to but perhaps less well-developed than those of extant forcipulate zoroasterids and asteriids. Vaulting of the actinostome cone effectively reduced space in the oral region, and consequently ossicles of the ambulacral and adambulacral series narrow toward the mouth, thereby maintaining ossicular and tube foot number in reduced space but dictating morphologic adjustments that might or might not be homoplastic among forcipulataceans.

As traditionally envisioned (e.g., Spencer & Wright 1966), the crown-group forcipulate subfamily Pedicellasterinae differs from the Asteriinae in that only two rows of tube feet can be present throughout the full arm length, and the adoral carina is weak or absent among pedicellasterids. A monophyletic pedicellasterid grouping failed to emerge in the analysis of Mah & Foltz (2011a), the genera interpreted as encompassing multiple basal lineages within the Forcipulatacea. The somewhat mixed expressions of trichasteropsids parallels that of traditional pedicellasterids, suggesting an early but analogous diversification complex, and again, the potential for disparity between ancient and extant.

The body wall skeleton of the new specimen of *Trichasteropsis?* sp., MPUM 8432, from Northern Grigna Mountain, Italy, is unfortunately largely obscured by spines, it nevertheless appearing apart from previously-described trichasteropsids and further documenting trichasteropsid diversity. The triangular arm tips of this specimen appear unlike

the enlarged distal arm intervals of *T. weissmanni*, suggesting a more basal positioning within the order.

The Triassic poraniid described by Blake et al. (2001) provides a useful marker of early crown-group diversity. It is emphasized that the new specimen from Slovenia described herein is very poorly preserved and therefore readily subject to differing interpretations; as noted in the description, its assignment to the Poraniidae is tentative, and that what little remains is only presented as “consistent” with poraniid affinities. A primary importance of the specimen is its documentation of asteroid presence in a new geographic setting, with the hope as is true of all rare occurrences, that added material will emerge. In parallel with his treatment of trichasteropsids, The non-forcipulatacean Poraniidae, well-represented in modern oceans, emerged near the base of a large group of non-forcipulatacean asteroids, although not immediately adjacent to the forcipulates in Mah & Foltz (2011b), and also stemward and therefore near to forcipulates in the phylogenetic sampling of Blake & Hagdorn (2003). Gale (2011) challenged assignment of Triassic *Noriaster* Blake et al., 2000, to the Poraniidae, assignment reviewed in Blake & Mah (2014).

## SYSTEMATIC PALEONTOLOGY

Class **ASTEROIDEA** de Blainville, 1830

Subclass **AMBULOASTEROIDEA**

Blake & Hagdorn, 2003

Infraclass **NEOASTEROIDEA** Gale, 1987

Diagnoses of the infraclass are available in Gale (1987, 2011, 2013) and Blake & Hagdorn (2003). Neoasteroids as now recognized are exclusively post-Paleozoic.

Superorder **Forcipulatacea** Blake, 1987

The taxonomy of the Forcipulatacea recently has been revised (Mah & Foltz 2011a).

Order **Trichasteropsida** Blake, 1987

The morphology of the Trichasteropsida indicates forcipulatacean affinities (Blake & Hagdorn 2003; Blake et al. 2006; Mah & Blake 2012; Blake & Mah 2014).

Family Trichasteropsiidae Blake & Hagdorn, 2003

*Trichasteropsis* Eck, 1879

***Trichasteropsis weissmanni*** (Münster, 1843)

Pl. 1, fig. 7-9; Pl. 2, fig. 2, 3

**Material:** Field Museum of Natural History FMNH PE 78510; stratigraphic position: mo3, Upper Muschelkalk, middle Ladinian, nodosus biozone, Bindlach, near Bayreuth, Germany; coll. 2008, Werner HERNUS, Erlangen, the specimen acquired through purchase, earlier illustrated by HILDNER (2010, p. 250). The specimen is exposed in ventral aspect, the mouth frame distended and the ambulacral furrows spread and flattened with burial, although the ossicles were not significantly pulled apart. Arm radii as preserved, 37, 30, 33, 40, and 39 mm, all arms truncated as interpreted relative to more complete *Trichasteropsis* specimens. Disk radii, extended as preserved, 23, 27, 23, 22, and 21 mm.

**Discussion.** A revised description of *T. weissmanni* was published in Blake & Hagdorn (2003) and augmented in Blake & Mah (2014); new information primarily on the jaw frame and axillary/odontophore are included above, and not repeated here.

***Trichasteropsis?* sp. indet.**

Pl. 1, fig. 1-6

**Material:** A single specimen exposed in ventral view from bed 28 of the UNIMI excavation (Tintori 2013) along the southern slope of the Northern Grigna Mountain, near the Como Lake (also known as Lario), 70 km north of Milano, Italy. The specimen is visible on the lower surface of a thin slab, thus it was buried in life position. The dorsal surface is embedded in a fine-grained calcarenite. The preparation was performed with a very thin sharp needle using very diluted formic acid under a binocular microscope by A.T. It is stored in the Museo di Paleontologia dell'Università degli Studi di Milano at Dipartimento di Scienze della Terra 'A. Desio', n. MPUM 8432. The age is Early Ladinian (Middle Triassic). Arm radii between about 27 and 30 mm; disk radii 7 to 10 mm. Although there is minor distortion, the specimen is essentially complete, with many adambulacral spines still in place. Ossicles are partially recrystallized and morphologic detail is not clearly preserved. Most *Trichasteropsis* specimens are late Anisian and early Ladinian in age.

**Description.** Disk small relative to elongate arms. Arm margins curved; distally, arms narrowing gradually, arm tips rounded. Interbranchial arcs angular. Ossicular debris of apparently relatively small actinal ossicles present in the interbranchia, but no marginals in evidence; actinal interbranchial ossicles not appearing aligned in rows. No body-wall ossicles recognized on arms beyond adambulacrals and spines. Madreporite unknown. Ambulacrals short, compressed, not flattened and leaf-like; podial pores well-defined. Adambulacrals short, wide, not

appearing alternately carinate, although expression largely obscured by spines. Individual mouth angle ossicles not clearly exposed but mouth angle pair appearing relatively small, narrow, parallel-sided. Ossicles immediately distal to MAO obscured by debris, but area confined, thereby indicating presence of few near-oral actinal ossicles. Adambulacral spines profuse, spine length approximately equaling width of parent adambulacral; spines robust, straight, tips pointed.

**Discussion.** The nature of the jaw frame, compressed ambulacral and adambulacral series, and simple, robust spine development identify the Trichasteropsiidae. The dorsal surfaces of the best-preserved specimens of *T. weissmanni* are arched, the arms rounded and columnar and the disk thickened, as is true of many extant asteriids. With burial, most *T. weissmanni* specimens collapsed, and the curved lateral walls were distorted, yielding exaggerated disk sizes. In MPUM 8432 spreading of proximal intervals of the ambulacra indicates some disk flattening, but in contrast with *T. weissmanni*, interbranchial ventral fields are small, and absence of arm ossicular debris beyond the adambulacrals favors a low profile in life. Preservation does not preclude presence of alternately carinate adambulacral, but furrow margins of the best-preserved intervals appear linear rather than alternate. Enlarged distal marginals are striking in *T. weissmanni*; there is no indication of such enlargement in MPUM 8432. The lack of specializations characteristic of other trichasteropsid taxa together with a Ladinian age favor stemward positioning for *Trichasteropsis?* sp. indet. in the Trichasteropsida.

Superorder **Valvatacea** Blake, 1987

Order **Valvatida** Perrier, 1884

Family Poraniidae? Perrier, 1893

Taxonomic terminology above follows Mah & Foltz (2011b).

Genus and species unknown

Pl. 2, fig. 1

**Material:** The specimen is housed in the Palaeontological collection Jurkovšek at Dol pri Ljubljani, Slovenia, registered at the Natural History Museum of Slovenia (abbreviated BJ) under the catalogue number 1417.

**Description.** Disk large, arms short, triangular, arm tips rounded. Body wall skeleton at most very poorly preserved but spathic calcitic? intervals are present at the edge of the disk of two interbrachia. Although partially obscured by putative calcified dermal material, rows of ossicles appear to be aligned with the edge of the disk of one interbrachium, not paralleling the ambulacral furrow adambulacral ossicles.

**Discussion.** The specimen is very poorly preserved and interpretation is difficult, leading to a tentative familial assignment; occurrence itself is an important new datum, hopefully stimulating search for additional, better-preserved material. What is available is consistent with poraniid affinities, including overall shape and occurrence of spathic calcite? intervals at the edge of the disk of two interbrachia, similarities reminiscent to expressions of the Jurassic poraniid of (Hess 1972), and both occurrences are in turn consistent with presence in life of reduced skeletons and heavy dermal tissue found in many extant poraniids. Reduced skeletons and heavy dermal layers are not unique to the Poraniidae (e.g., Mah 2003), but they are common among poraniids and uncommon or rare among other taxa.

In extant poraniids and forcipulates, the ventral, actinal ossicles are aligned with the marginal series whereas in other crown-group asteroids, actinal alignment is with the adambulacral series (Hotchkiss & Clark 1976); although poorly preserved, marginal alignment appears to be present in one interbrachium of the Slovenian specimen. In addition to the Middle Jurassic poraniid of Hess (1972), a Norian (Late Triassic) species was described by Blake et al. (2000), the Late Triassic Carnian age of the Slovenian example immediately pre-dates the Norian, thereby at least potentially extending familial range.

## OCCURRENCE AND PALEOENVIRONMENT

The new specimen of *Trichasteropsis weissmanni* is from the Upper Muschelkalk, Middle Triassic Ladinian mo3 nodosus biozone, at Bindlach, Bavaria, Germany. The multiauthored chapter on the Triassic (McCann 2008) provided a recent detailed overview of the Muschelkalk, and Aigner & Bachmann (1992) placed the Muschelkalk and the remainder of the German Triassic in a stratigraphic framework; Blake & Hagdorn (2003) focused on the occurrence of *Trichasteropsis*.

The European platform of the three-fold Muschelkalk was a geologically and geographically complex region of advancing and retreating seaways and intergrading environments that were situated toward the northwestern tip of the broadly triangular Tethys Seaway, the region one of relatively hot and arid conditions; Muschelkalk sediments that accumulated in this setting are complex as well, but represent relatively shallow, well-oxygenated conditions. The Muschelkalk is divided into three intervals, the Upper and Lower consisting broadly of fossiliferous carbonates, the Middle of unfossiliferous dolostones and evaporitic sediments. Although a relatively rare fossil, *Trichasteropsis* is widely distributed through both the Upper and Lower Muschelkalk, but lacking from the middle, barren interval, and therefore although known occurrences of *Trichasteropsis* are limited to the European platform, it must have invaded the region from other areas at least twice. Few Triassic asteroids have been de-

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## PLATE 1

Figs 1-6 - *Trichasteropsis?* sp. indet., MPUM 8432.

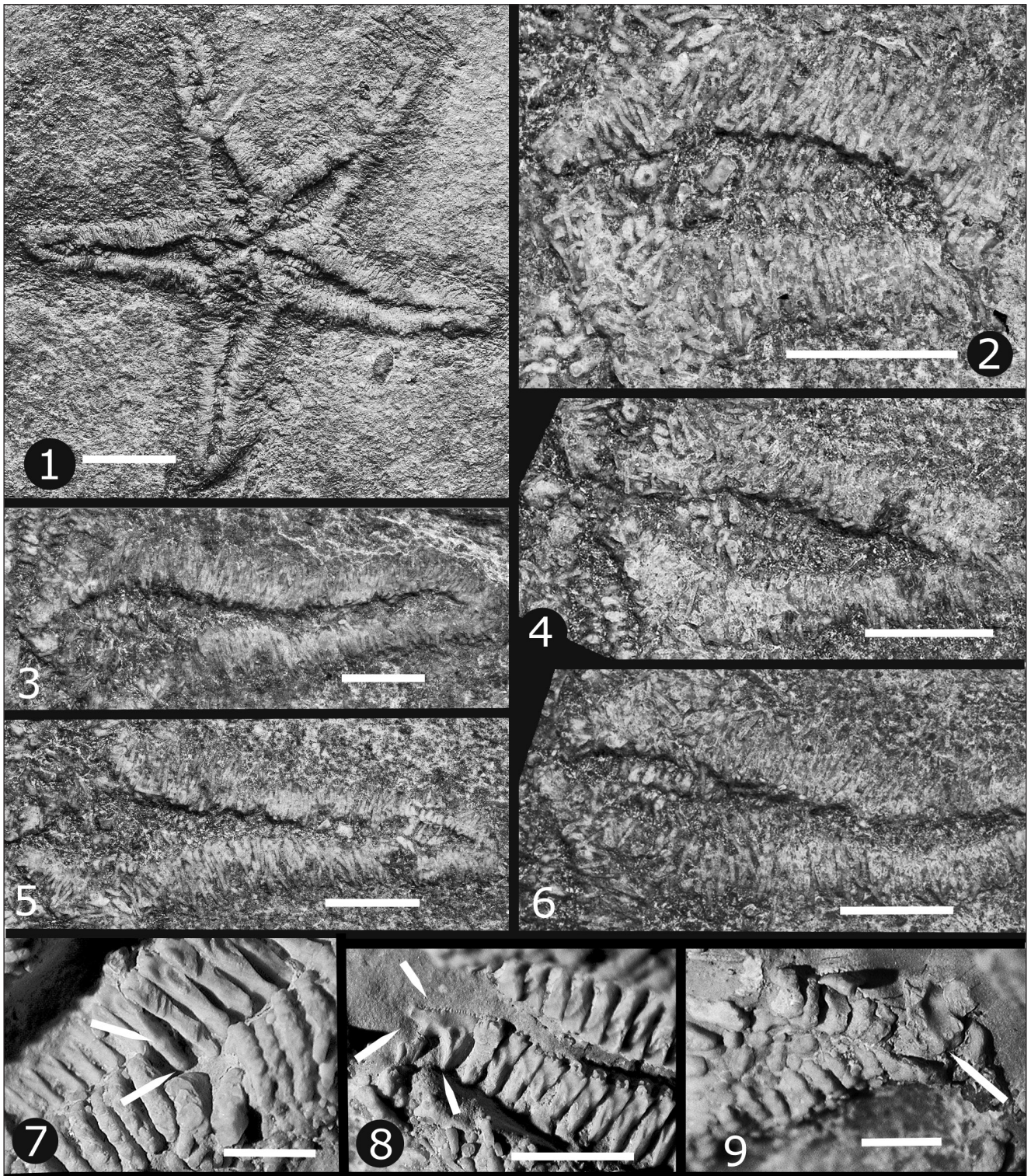
- 1) Ventral view; specimen little distorted by sediment compaction.
- 2) Proximal interval of arm to upper left of Fig. 3A showing spines, obscured adambulacrals and mouth frame ossicles; short or compressed ambulacral ossicles visible in dilated mid-arm interval; interbrachial ossicles largely obscured.
- 3) Downwardly directed arm of 3A showing arm outline, spines, jaw frame; interbrachial and ambulacral ossicles largely obscured by debris.
- 4) Proximal interval of arm to upper right of 3A showing jaw frame ossicles, interbrachial ossicles, parts of ambulacral ossicles.
- 5) Arm to left of 3A showing arm shape, spines, distal ambulacrals, interbrachia.
- 6) Arm to lower right of 3A showing arm form, mouth frame, adradial portion of proximal ambulacrals.

Figs 7-9 - *Trichasteropsis weissmanni*, FMNH PE 78510.

- 7) Distal portion of ambulacral column. Ambulacral-adambulacral articular surface (arrows at termini) ventrally directed, abutted adambulacral as in asteroiids, but did not extend fully across adambulacral. For positioning, see Pl. 2, fig. 2, 3.
- 8) Circumoral, cross-furrow articular facets (upper arrow); open podial pore and contact surface between circumoral and MAO (lower left arrow); approximate contact between transverse ridge of circumoral and MAO, also ovate cross-furrow muscle depression, the podial pore in a shadow (lower right arrow). On ambulacral beyond mouth frame, the ossicular cross-furrow muscle depressions are deflected toward the mouth and cross-furrow articular faceting is robust. For positioning, see Pl. 2, fig. 2, 3.
- 9) Lateral view of robust MAO, it twisted out of alignment with adambulacrals; MAO ventral edge with spine bases (arrow). For positioning, see Pl. 2.2, 2.3.

Scale bars equal 10 mm (fig. 1), 5 mm (figs 2-6), and 3 mm (figs 7-9).



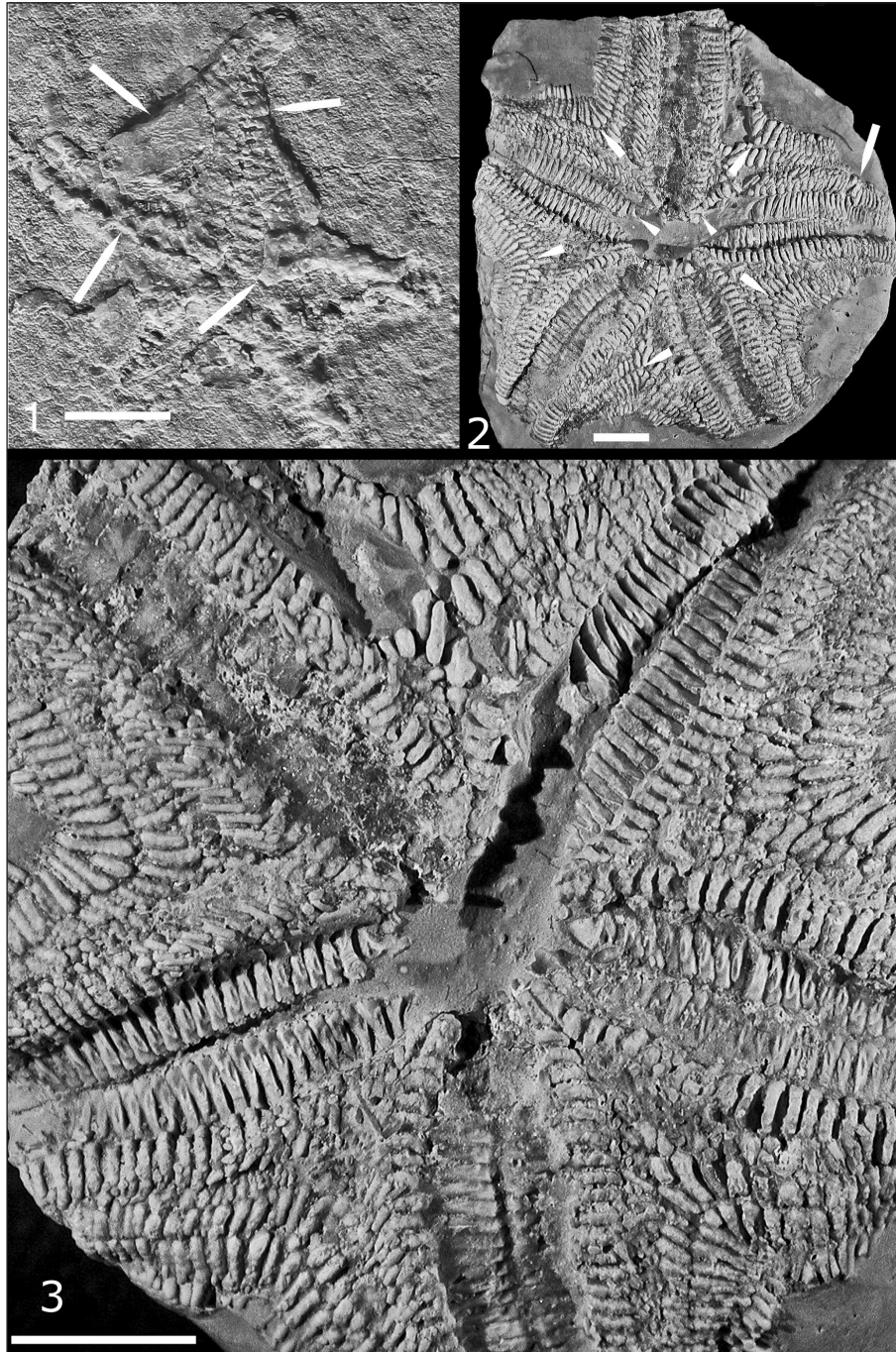


scribed (Blake & Hagdorn 2003), but recurrence of *Trichasteropsis* suggests a largely unknown asteroid presence during Triassic times.

The nodosus biozone interval of the Bindlach specimen is thought to represent the highstand of the Upper Muschelkalk. The nodosus interval lacks the inferred rather strictly stenohaline crinoids and

echinoids, and conodonts and ceratite ammonoids are endemic; the interval therefore is thought to have been limited to organisms of broader salinity tolerances. Nevertheless, the *T. weissmanni* setting likely was closer to the life habitat of the Italian *Trichasteropsis?* sp. indet. than to the apparently restricted basin occurrence of the Slovenian poraniid sp. indet.





## PLATE 2

Fig. 1 - Family Poraniidae? BJ 1417. Calcitic rind at disk margin suggesting mineralized dermal tissue (upper left arrow); alignment suggestive of actinal ossicles parallel to disk edge (upper right arrow); calcitic rind on ambulacrals (lower left arrow); mouth angle ossicular pair (lower right arrow).

Fig. 2-3 - *Trichasteropsis weissmanni* (Münster), FMNH PE 78510. 2) Ventral view of complete specimen, the disk somewhat distended by sediment compaction; five arrows at adradial edges of marginal series at all interbranchial midlines indicating apparent axillaries; upper right arrow identifying position of Pl. 1, fig. 7; left arrow at mouth frame identifies Pl. 1, fig. 8, inverted; right arrow at mouth frame identifies Pl. 1, fig. 9, inverted. 3) Enlargement of mouth frame and proximal arm intervals of FMNH PE 78510 rotated approximately 45 counterclockwise from Pl. 2, fig. 2, note positioning of barren area of upper right interbranchium of figure 2, unmarked by arrows for clarity. Ambulacrals of some furrows partially obscured by secondary mineralization; ambulacral and adambulacral series narrowing toward mouth; adambulacrals alternately carinate.

Scale bars equal 5 mm (fig. 1) and 10 mm (figs 2, 3).

A number of *Trichasteropsis* genera and species have been described from the Muschelkalk (Blake & Hagdorn 2003; herein), although the *T. weissmanni* configuration clearly is the dominant. *Trichasteropsis weissmanni* has been recognized from varied muddy, shelly, and oolitic substrates; nevertheless, because of the scanty record and complex character expressions typical of many asteroids, it cannot be determined if more than one biospecies might be represented by the *T. weissmanni* morphologic facies.

The Italian *Trichasteropsis?* sp. indet. specimen comes from an area where Middle Triassic fossils,

both vertebrates and invertebrates, have been collected and studied since the first half of the 19th Century. The Grignas geographically belongs to the Prealpi Lombarde, which lie to the east of Como (Lario) Lake. The Grigna group consists of three overlapping thrusts, each constituting one of the three most important mountaintops of the group, the Northern Grigna (locally called also Grignone, the Big Grigna) being the highest. The Buchenstein Formation is present only in this northern block, and it crops out along the southern slope of the mountain. It consists essentially of regularly strati-

fied limestone, with bed thicknesses between 10 and 30 cm, these locally laminated or somewhat marly. The color is usually light-grey/brown at weathered surfaces and dark grey to black in fresh fractures. The lower part of the unit is somewhat nodular, although the fossiliferous horizon is made of planar beds, and contains lenses or thin beds of black chert; interbeds are clayey or clayey-marl with tuffaceous joints. Intercalations of light-yellow, orange, or red pyroclastics ranging in thickness from one to about 40 cm occur. The total thickness of the unit in the N. Grigna area ranges from 100 to 150 meters. The Esino Formation locally overlies the Buchenstein (Fig. 2A), the stratigraphic boundary marked by a gradual transition from stratified limestone to massive white limestone, the transition marking the filling of the basin by progradation of the carbonate platform.

The depositional environment of the Buchenstein Formation was in a quiet, relatively deep intra-platform basin marked by more or less extended low oxygen to anoxic events. The deep basin was bordered by the carbonate platform of the Esino Formation; thin bioclastic debris flows washed into the basin from the nearby carbonate platform to accumulate along the slope in quiet, oxygen-poor settings, the debris possibly incorporating benthic organisms such as *Trichasteropsis* sp. indet.

Conodont dating, based on the presence of *Pseudofurnishius priscus* Sadeddin, 1990 and *Budorvignathus troempyi* (Hirsch, 1971), indicates the Fasnian (upper *curionii* zone), which is not far from the Anisian-Ladinian boundary (Nicora & Rusconi 2007). From this fossiliferous horizon, more than 1500 fish remains have been collected during five years of excavation. Several interesting nectobenthic subholosteans, such as *Stoppania* and *Ctenognathichthys* (Lombardo et al. 2008) have been collected, as well as several very large (up to more than 1 m) *Saurichthys* (Tintori 2013). Many very small fishes are found on mass mortality surfaces, implying sudden changes in the environmental conditions, possibly related to the volcanic activity as suggested by the presence of thin cineritic layers (Pasquarè & Rossi 1969 and A.T. pers. obs.). Relatively rare decapod crustaceans (A.T. pers. obs.) and thylacocephalans also have been found, the latter being the only strictly benthic organism other than *Trichasteropsis* sp. indet. Other complete macrobenthos remains are very rare, including only a few fragments of

bivalves other than *Daonella*. Brachiopods and crinoids have been recorded, though the rock matrix can be considered mostly as a biocalcarene.

The Slovenian fossil was collected from bituminous cherty limestone in the Vrata Valley (Fig. 2B) of the northern part of the Julian Alps, Slovenia. The Vrata Valley lies below Triglav Mountain, which structurally forms the eastern part of the Southern Alps (Jurkovšek 1987a, 1987b; Placer 1999, 2008; Buser et al. 2008). The Slovenian part of the Julian Alps formed an isolated platform between the Slovenian Basin and the Hallstatt–Meliana Ocean (e.g. Haas et al. 1995; Ziegler & Stampfli 2001; Stampfli & Borel 2002). The stratigraphic sequence is thought to represent an intrashelf setting along a platform slope; circulation was restricted and water masses varied from oxic to disoxic (Haunold et al. 1999). A Carnian, *polygnathiformis* Zone determination is based on the conodont fauna (Kolar-Jurkovšek 1991), the setting a little younger than the *Trichasteropsis* specimens discussed here.

Platy limestones with chert in the Vrata Valley show a complex sedimentary history, as they were deposited in an oxygen-depleted environment with multiphase platform progradation (Schlaf et al. 1997a, 1997b, 1999; Celarc & Kolar-Jurkovšek 2008). The 80-meters sequence accumulated under an extremely high sedimentation rate of 400 mm/ka (Schlaf 1997), pointing to accelerated subsidence accompanying synsedimentary faulting. Presence of reducing seawater/sediment interface conditions is based on rare-earth (REE) concentrations, including a high  $Ce_n/La_n$  ratio (Haunold et al. 1999), incorporated in the conodonts.

Vrata Valley strata yields abundant, well-preserved specimens of the bivalve *Halobia* published by (Kittl 1912). During geological mapping for the Basic Geological Map of Yugoslavia 1:100,000, the Beljak (Villach) and Pontebba sheet (Jurkovšek 1987a, b), several excellently preserved fossils were collected, the most important of the vertebrates an 84 cm skeleton of a birgeriid fish (Jurkovšek & Kolar-Jurkovšek 1986), it collected in association with cranial bones of *Saurichthys*. Invertebrate fossils include decapod crustaceans (Jurkovšek & Kolar-Jurkovšek 1992), ammonoids, the inarticulate brachiopod *Discinisca* (Bitner et al. 2010), echinoids, and the poraniid? sp. indet. treated here. Presence of discinisca brachiopods might indicate at least local or temporary oxygenated bottom conditions.



The locality is treated in more detail in Bitner (2010). Presence of at least temporary reducing conditions at the sea floor has been based on preservation of soft-bodied organisms such as the worm *Valvasoria carnio-lica* Kolar-Jurkovšek & Jurkovšek (Kolar-Jurkovšek & Jurkovšek 1997; Celarc & Kolar-Jurkovšek 2008), articulated fish such as the large *Birgeria*, and the asteroid.

Finally, at least one as yet undescribed asteroid specimen has been reported from the Anisian of southern China (Benton et al. 2013). The Luoping Fauna, although mostly known for its marine vertebrate assemblage, has also yielded a few invertebrates. Arthropods and gastropods are usually common in the Upper Vertebrate Horizon (Sun et al. 2009; A.T. pers. obs.), while echinoderms are very rare, including a single crinoid from the Lower Vertebrate Horizon and the as yet undescribed asteroid. The asteroid specimen is from the Upper Vertebrate Horizon (Benton et al. 2013), where it is associated with common gastropods, thereby recording a possible nearby oxygenated bottom. The level yielding the Luoping Fauna is about 20 m thick and it is bracketed between massive limestones/dolostones of a shallow-water carbonate platform (Upper Member of the Guanling Formation, including the fossiliferous level, and the overlying Yangliujing Formation). This anoxic basinal facies crops out for about 200 km<sup>2</sup> in the area around the village of Dawasi (Benton et al. 2013). Rarity of pelagic fauna, such as ammonoids and ichthyosaurs, witnesses a poor connection to the open waters of the Nanpanjiang Basin to the southeast. Also, the presence of several fish and arthropods mass mortality surfaces (Sun et al. 2009) prove that the paleoenvironment could be at least temporarily toxic. Oxic bottom surrounded the anoxic bottom lagoon, although the scarce and oligotypic benthic fauna witnesses presence of harsh conditions in shallow waters.

## CONCLUSIONS

In conclusion, we record the presence of Middle/Late Triassic asteroids in the German Basin and in different sites of the Tethys, from the west (now southern Alps) to the east (now southern China). Triassic asteroids are rare on a global basis, and although they occur widely in the Muschelkalk, they are not numerically abundant. Earlier reports of all

Triassic asteroids as well as those specifically of the Muschelkalk were summarized by Blake & Hagdorn (2003). Overall, fossil asteroids are relatively infrequently encountered in the geologic record, perhaps largely because their construction is comparatively delicate and readily destroyed by taphonomic processes, unlike, for example, the comparatively robust construction more typical of mollusks. Nevertheless, in addition to Muschelkalk occurrences, more common asteroid specimens and fragments have been recorded from a number of stratigraphically and geographically widely distributed sites, including the Devonian Hunsrück Slate of Germany (e.g., Lehmann 1957), the Jurassic and Cretaceous of France (e.g., Breton 1992), and the Eocene of Antarctica (e.g., Blake & Aronson 1998), and for each of these occurrences, local setting and history appears to have at least temporarily favored asteroid preservation.

Both later Paleozoic and early Mesozoic asteroids are particularly rare, but fairly distinctive, suggesting a possible Triassic recovery from a time of crisis. Paleoenvironmental conditions between the Alpine and Chinese sites are parallel, including presence of fine, shallow-water micrite and/or biocalcarene as well as similarities of paleotopography (intra-carbonatic platform basins). It is worth also to note that Alps (then western Tethys), and southern China (East Tethys) belonged to the same paleobio-province during the Middle/early Late Triassic, as it is proved by several arthropods, fishes and marine reptiles that were present at both ends of the Tethys (Taylor, Schram & Yan-Bin 2001; Lin et al. 2011; Lombardo et al. 2011; Ji et al. 2014). Beyond these similarities, a potentially important difference appears to be the latitude, the German Muschelkalk having accumulated at a more northern setting than both the Southern Alps and South China Block, and thus in a more temperate climate. This as well as a stronger clastic influx from extended emerged land could also explain the lack of carbonatic platform in the German Basin. Following the late Paleozoic-early Mesozoic crisis and extinctions, perhaps radiating asteroid clades preferred temperate to more tropical waters. An analogy might be found in the modern Asteriidae (e.g., *Asterias*), the family abundant in higher latitudes today, but comparatively uncommon at low latitudes (e.g., Fisher 1930; Clark & Rowe 1971). The Asteriidae, like the Trichasteropsida, is a member of the superorder Forcipulatacea (Blake & Hagdorn, 2003).

*Note added in proof.* The following study appeared too late to be treated in the present paper; although well worthy of comparative interpretation, essential viewpoints expressed here are retained.

Villier L., Brayard A., Bylund K.G., Jenks J.F., Escarguel G., Olivier N., Stephen D.A., Vennin E. & Fara E. (2017) - *Superstesaster promissor* gen. et sp. nov., a new starfish (Echinodermata, Asteroidea) from the Early Triassic of Utah, USA, filling a major gap in the phylogeny of asteroids. *J. Syst. Palaeontol.*, 2017 <https://doi.org/10.1080/14772019.2017.1308972>

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