

# A new species of *Dapedium* LEACH, 1822 (Actinopterygii, Neopterygii, Semionotiformes) from the Early Jurassic of South Germany

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## Abstract

Deep-bodied specimens of *Dapedium* LEACH, 1822 from the Lower Jurassic (Upper Liassic; Early Toarcian) *Posidonia* Shale from the Holzmaden area, southern Germany bearing serrated scales were traditionally identified and labelled as *D. punctatum* AGASSIZ, 1835. These specimens differ, however, from the holotype of this species known from the older Lower Liassic (Sinemurian) of England and do not belong to *D. punctatum*. Comparison of the specimens concerned with the contemporaneous *D. pholidotum* (AGASSIZ, 1832), *D. magnevillei* (AGASSIZ, 1836), *D. caelatum* QUENSTEDT, 1858, and *D. milloti* SAUVAGE, 1891 as well as with other Liassic species of *Dapedium* shows that the Upper Liassic specimens of so-called “*D. punctatum*” in fact represent a new species, which is described here and named *Dapedium stollorum* n. sp. The diagnoses of Dapediidae LEHMAN, 1966 and *Dapedium* LEACH, 1822 are amended, and reconstructions of the Early Toarcian *Dapedium* are presented.

**Key words:** Osteichthyes, Actinopterygii, Neopterygii, Semionotiformes, *Dapedium*, Lower Jurassic, Early Toarcian, Sinemurian, *Posidonia* Shale, south Germany, England.

## Zusammenfassung

Tiefbauchige Vertreter der Gattung *Dapedium* LEACH, 1822 mit gezähnelten Schuppen aus dem Posidonienschiefer (Unterjura, Unter-Toarcium) S-Deutschlands wurden traditionellerweise der Art *D. punctatum* AGASSIZ, 1835 zugeordnet. Diese Exemplare unterscheiden sich jedoch vom Holotyp dieser Art aus dem Unterlias (Sinemurium) von England. Der Vergleich der betreffenden Exemplare mit den gleichaltrigen oberliassischen Arten *D. pholidotum* (AGASSIZ, 1832), *D. caelatum* QUENSTEDT, 1858, *D. milloti* SAUVAGE, 1891 und *D. magnevillei* (AGASSIZ, 1836) sowie mit anderen *Dapedium*-Arten aus dem Lias zeigt, dass die „*D. punctatum*“-Exemplare aus dem oberliassischen Posidonienschiefer zu einer neuen Art gehören. Diese neue Art wird hier unter dem Namen *Dapedium stollorum* n. sp. beschrieben. Daneben werden die Familiendiagnose von Dapediidae LEHMAN, 1966 und die Gattungsdia­gnose von *Dapedium* LEACH, 1822 verbessert, und es werden Rekonstruktionen vom oberliassischen *Dapedium* vorgestellt.

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## 1. Introduction

*Dapedium* LEACH, 1822 is a neopterygian genus containing deep-bodied fishes of medium size that were first discovered by early 19<sup>th</sup> century fossil collectors at the famous Lower Liassic outcrops at Lyme Regis, southern England. In 1835 AGASSIZ changed the spelling of the generic name into the masculine form *Dapedius*, by which the taxon subsequently became widely known. AGASSIZ (1835a: 181) did so because he adopted masculine endings for all names of fish genera he described. Recent scholars (e. g., THIES 1988, THIES et al. 2008) have returned to the original spelling of *Dapedium* for reasons of priority.

The stratigraphical range of the genus is restricted to approximately 25 My from the Late Triassic (Rhaetian) to the Earliest Middle Jurassic (Earliest Aalenian, SCHMIDT

1919, pers. comm. R. BÖTTCHER). The geographical distribution includes Europe and India (LEHMAN 1966, JAIN 1973, TINTORI 1983) encompassing the Mesotethys seaway.

In Germany the genus is represented by three species from the Upper Liassic (Early Toarcian) *Posidonia* Shale of southern Germany: *D. caelatum* QUENSTEDT, 1858, *D. pholidotum* (AGASSIZ, 1832) and “*D. punctatum* AGASSIZ, 1835”. THIES (1988) and THIES et al. (2008) pointed out taxonomical problems related to these species and described a neotype for *D. caelatum*. Specimens of *Dapedium* from the *Posidonia* Shale identified as *D. punctatum* by QUENSTEDT (1858) were already suspected of not being conspecific with *D. punctatum* AGASSIZ, 1835 from the Lower Liassic (Sinemurian) of England by WAGNER as early as 1860. However, WAGNER’s view was ignored by later palaeontologists. So, even today certain specimens

of *Dapedium* from the Upper Liassic *Posidonia* Shale are still considered as belonging to *D. punctatum* AGASSIZ, 1835. This refers, for example, to specimens housed in the collections of the Staatliches Museum für Naturkunde, Stuttgart, and the Museum Hauff, Holzmaden (URLICHS et al. 1979, HAUFF & HAUFF 1981). Comparison with the holotype of *D. punctatum* in the Oxford University Museum of Natural History, England, has shown, however, that the south German specimens actually differ from the Lower Liassic (Sinemurian) *D. punctatum*, among others, in tooth and scale morphology and thus represent a so-far-undescribed species. This new species of *Dapedium* is described in this paper.

#### Anatomical abbreviations

Ang	angular
Ant	antorbital
Apal	autopalatine
apl	anterior pit line of the skull roof
Art	articular
awen	anterior wall of the endochondral neurocranium
bp	basipterygoid process
Br	branchiostegal rays
Ch	ceratohyal
Cl	cleithrum
Co	coronoid
De	dentary
Dpal	dermopalatine
DPF	complex bone formed by fusion of the dermopterotic, parietal and frontal
Dpt	dermopterotic
Dsp	dermosphenotic
en	endochondral neurocranium
Entp	entopterygoid
epen	ethmoidal part of the endochondral neurocranium
Exsc	extrascapular
fi	interorbital fenestration
fHym	articular facet for the hyomandibula
Fr	frontal
Gu	gular
Hh	hypohyal
hpl	horizontal pit line of the cheek
Hym	hyomandibula
Io	infraorbital
Iop	interoperculum
Le	lepidotrich, lepidotrichia
Md	mandibula
mpl	median pit line of the skull roof
Mr	“middle region” of the endochondral pectoral girdle
Mtp	metapterygoid
Mx	maxilla
Na	nasal
na(1)	anterior nasal opening
na(2)	posterior nasal opening
Op	operculum
open	occipital part the endochondral neurocranium
Pa	parietal
Part	prearticular
pbas	basisphenoidal part of the endochondral neurocranium
Pcl	postcleithrum

pcpllt	pores of the cephalic portion of the lateral line of the trunk
pec	pores of the ethmoidal commissure
phbioc	pores of the horizontal branch of the infraorbital canal of the cheek
pioc	pores of the infraorbital canal
plgu	gular pit line
plmd	mandibular pit line
plsl	pit line on the supracleithrum
pmdc	pores of the mandibular canal
Pmx	premaxilla
Pop	preoperculum
popen	postorbital process of the endochondral neurocranium
ppen	postorbital part of the endochondral neurocranium
ppoc	pores of the preopercular canal
pQu	process of the quadrate for the articulation of the lower jaw
Ps	parasphenoid
psc	pores of the supraorbital canal
Psc	presupracleithrum
pstc	pores of the supratemporal commissure
Pstt	posttemporal
pvbioc	pores of the vertical branch of the infraorbital canal of the cheek
Quj	quadratejugal
Ra	radial
Rb	branchiostegal rays
Ro	rostral
Sang	supraangular
Sang+Ang	co-ossification of the supraangular and the angular
Scl	supracleithrum
si	interorbital septum
Smx	supramaxilla
So	suborbital
son	base of the nasal cavity
Sop	suboperculum
Spl	splenic
Spo	supraorbital
stpl	supratemporal pit line
vpl	vertical pit line of the cheek
(l)	left
(r)	right
(?)	questionable identification

#### Acronyms of repositories

GPIT	Paläontologische Forschungs-, Lehr- und Schausammlung, Institut für Geowissenschaften der Universität Tübingen, Germany
OMNH	Oxford University Museum of Natural History, England
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
UHH	Urweltmuseum Hauff Holzmaden, Germany

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the stratigraphic range of the genus *Dapedium* with us. Dr. S. TURNER (Brisbane) gave valuable comments and improved the English. Dr. A. LÓPEZ-ARBARELLO (Munich) carefully reviewed the manuscript and also commented on it. R. B. H. thanks Drs KURT and WILFRIED STOLL for financial support for the preparation of *Dapedium* specimens. This research was funded by the Deutsche Forschungsgemeinschaft (DFG, grant TH 394/8-1)

## 2. Systematic palaeontology

Division Halecostomi REGAN, 1923

Order Semionotiformes ARAMBOURG & BERTIN, 1958

Family Dapediidae LEHMAN, 1966

**Diagnosis** (after LEHMANN 1966, amended). – Small to medium-sized fishes (up to at least 450 mm standard length), body deeply fusiform to nearly circular in outline and compressed laterally; circumorbital bones comprising a series of infraorbitals and a series of suborbitals; vertical branch of preoperculum covered by suborbitals to a varying extent; dorsal and anal fin hem-like.

**Remarks**. – LEHMAN (1966) used the family Dapediidae in order to separate deep-bodied semionotiforms from those with a fusiform body which he included in the family Semionotidae. He defined the order Semionotiformes by the following characters (LEHMAN 1966: 156):

- suspensorium vertical ou incliné vers l'avant
- bouche petite
- nombreux os infraorbitaux
- dents le plus souvent broyeuruses, en particulier sur les os du palais
- os de la tête et écailles épais
- le squelette axial comprend des vertèbres non ossifiées ou en anneaux ou en demi-anneaux
- les nageoires présentent des fulcres très développés
- le bord dorsal du corps est en général déprimé sous la nageoire dorsal
- écailles le plus souvent rhombiques

The Semionotidae are then characterised by “l'aspect du corps plus ou moins fusiforme” (LEHMAN 1966: 157). By contrast, in the Dapediidae “le corps est comprimé latéralement” (LEHMAN 1966: 163). Whereas the ideas on the systematics and relationships of the order Semionotiformes and the family Semionotidae were enhanced by later authors (WENZ 1968, 1999, PATTERSON 1973, OLSEN & McCUNE 1991, GARDINER 1993, GARDINER et al. 1996, BRITO 1997, CAVIN & SUTEETHORN 2006, LÓPEZ-ARBARELLO 2006) the Dapediidae were not reconsidered since LEHMAN (1966). OLSEN & McCUNE (1991) recognised a series of apomorphic characters for the Semionotiformes but excluded the Dapediidae from this order. The diagnostic characters of the Semionotiformes put forward by LEHMAN (1966) differ from those proposed by OLSEN & McCUNE (1991) and seem to be, in fact, all primitive. The possession of

dapediids of a laterally compressed body (LEHMAN 1966) is certainly also a plesiomorphic feature leaving the Dapediidae still undefined. A survey of published records on deep-bodied semionotiforms has resulted in the amended family diagnosis above which in the absence of a cladistical analysis can only be preliminary. A cladistical analysis of deep-bodied semionotiforms is, however, beyond the scope of this study.

Genera included:

*Dapedium* LEACH, 1822 from the Late Triassic to the Earliest Middle Jurassic of Europe, type genus (GARDINER 1960, THIES 1988, TINTORI 1983, WENZ 1968, WOODWARD 1895);

*Paradapedium* JAIN, 1973 from the Lower Jurassic of India (JAIN 1973);

*Sargodon* PLIENINGER, 1847 from the Late Triassic of Europe (TINTORI 1983);

*Heterostrophus* WAGNER, 1863 from the late Jurassic of Europe (EASTMAN 1914 (as *Homoeolepis*), LAMBERS 1999, WOODWARD 1929);

*Dandya* WHITE & MOY-THOMAS, 1940 from the Late Triassic of Europe (GORJANOVIC-KRAMBERGER 1905 (as *Spaniolepis*), TINTORI 1983);

*Tetragonolepis* BRONN, 1830 from the Early Jurassic of Europe and India (GARDINER 1960, JAIN 1973, THIES 1991);

*Hemicalypterus* SCHAEFFER, 1967 from the Late Triassic of North America (SCHAEFFER 1967)

### Genus *Dapedium* LEACH, 1822

**Type species**: *Dapedium politum* LEACH, 1822 from the Lower Liassic (Sinemurian) of England (Lyme Regis).

**Synonymy**: See WOODWARD (1895: 128), GARDINER (1960: 299), THIES (1988: 91)

**Diagnosis** (after WENZ 1968, amended). – One supramaxilla present; up to three tooth-bearing coronoids; coronoids taking part in the formation of the dorsal edge and the dorsolateral cover of the lower jaw; lateral coronoid teeth large, styliform and continuing caudally the marginal row of dentary teeth; number of branchiostegal rays between four and eight; dermal bones of skull roof, cheek and lateral side of lower jaw heavily ornamented by ganoin tubercles and ridges, infraorbital canal below the orbit with a vertical and a horizontal branch sometimes being replaced by pit lines on the infraorbitals and suborbitals.

**Remarks**. – WENZ (1968: 79) based on WOODWARD (1895: 128–133) diagnosed the genus *Dapedium* LEACH, 1822. The characters listed by her, however, are either not apomorphic or do not occur in all species of *Dapedium* or do not apply to the species of *Dapedium* at all. For example, WENZ considered the hem-like antero-caudal prolongation of the dorsal and anal fins as well as the hypsomatic body as derived characters of *Dapedium*, but these features also occur in the other dapediid genera listed above. Furthermore, WENZ emphasized the fusion of elements of

the infra- and suborbital series behind the orbit. This concerns *D. pholidotum* but is missing in *D. caelatum*, in the specimens described here and in Lower Liassic species of *Dapedium* (THIES 2008, WENZ 1968). WENZ also stated that *Dapedium* lacks a supramaxilla. This is not correct. A supramaxilla was repeatedly reported to occur in *Dapedium* (PATTERSON 1973, WOODWARD 1895, see below).

We have to admit that we are likewise unable to identify apomorphic characters for *Dapedium* LEACH, 1922 in the literature data. This might be because the genus as currently understood contains numerous species and might not be monophyletic. At least 20 species are now referred to the genus, 19 of which were described first in the 19<sup>th</sup> century and these early descriptions no longer meet modern taxonomical requirements. Nevertheless, we think that the suite of characters listed in the amended generic diagnosis above is helpful in separating *Dapedium* from the other dapediid genera. For a better understanding of *Dapedium* LEACH, 1822, a revision of the genus, which is urgently needed, is still awaited (THIES 1988, TINTORI 1983).

*Dapedium stollorum* n. sp.

Figs. 1–9, Pls. 1–4

- 1929 *Dapedius*. – BERCKHEMER 1929, p. XXIX.  
 1930 *Dapedius*. – SCHWENKEL 1930, pp. 24–25, fig. 5.  
 1953 *Dapedius punctatus* AG. – HAUFF 1953, p. 47, pl. 47.  
 1979 *Dapedium*. – URLICHS et al., p. 22, fig. 25.  
 1981 *Dapedium punctatum* (AG.). – HAUFF & HAUFF, p. 72, fig. 83.  
 1988 *Dapedium*. – CARROLL, p. 107, fig. 6–26.  
 1988 *Dapedium punctatum*. – THIES, p. 107, fig. 6b.  
 1993 *Dapedium*. – CARROLL, p. 117, fig. 6–26.  
 1994 *Dapedium*. – WILD, pp. 70–71, fig. 81.  
 1998 *Dapedium*. – BÖTTCHER, p. 92, fig. 7.20.  
 1999 *Dapedium punctatum* AGASSIZ 1835. – THIES & HERZOG, pp. 145, 146, figs. 1C, 2.  
 2003 *Dapedium*. – URLICHS & ZIEGLER, p. 255, fig. p. 255.

**Derivation of name:** After Drs KURT and WILFRIED STOLL in honour of their many contributions and donations to the Urweltmuseum Hauff Holzmaden.

**Holotype:** SMNS 16219, a complete and articulated adult specimen shown in Figs. 1–4A and Pl. 1.

**Locality:** Abandoned and refilled quarry at Holzmaden, Baden Württemberg, southern Germany.

**Age:** Early Jurassic, Early Toarcian, Tenuicostatum Zone.

**Horizon:** “Fleins” within the south German *Posidonia* Shale (Lias  $\epsilon$  II<sub>1</sub>) (URLICHS et al. 1979).

**Additional material:**

**Paratype 1:** UMH 3, a complete and articulated adult specimen shown in Figs. 5–6 and Pl. 2.

**Locality:** Abandoned and refilled quarry in the Holzmaden/Ohmden area, Baden Württemberg, southern Germany.

**Age:** Early Jurassic, Early Toarcian, Tenuicostatum Zone.

**Horizon:** “Fleins” within the south German *Posidonia* Shale (Lias  $\epsilon$  II<sub>1</sub>).

**Paratype 2:** UMH 35, a complete and articulated adult specimen shown in Figs. 7–8 and Pl. 3.

**Locality:** Abandoned and refilled quarry in the Holzmaden/Ohmden area, Baden Württemberg, southern Germany.

**Age:** Early Jurassic, Early Toarcian, Tenuicostatum/Falciifer Zone.

**Horizon:** “Unterer Schiefer” within the south German *Posidonia* Shale (Lias  $\epsilon$  II<sub>4</sub>).

**Paratype 3:** UMH 19, a complete and articulated semi-adult specimen shown in Figs. 4B, 9 and Pl. 4.

**Locality:** Abandoned and refilled quarry in the Holzmaden/Ohmden area, Baden Württemberg, southern Germany.

**Age:** Early Jurassic, Early Toarcian, Bifrons Zone.

**Horizon:** “Wilder Schiefer” within the south German *Posidonia* Shale (Lias  $\epsilon$  III).

**Remarks.** – The localities of the types of the new species cannot be specified in greater detail. The specimens were recovered in the first half of the 20<sup>th</sup> century from small temporary quarries which were opened in the *Posidonia* Shale of the Holzmaden/Ohmden area in order to produce mineral oil from the bituminous shale by smouldering. Later, the horizons “Fleins” and “Tafelfleins” within the *Posidonia* Shale succession were dug out mainly. Rocks from these horizons were used for interior decoration purposes such as production of desk tops and reveals for windows and doors. All of these quarries in the *Posidonia* Shale of the Holzmaden/Ohmden area existed only for a short time and their exact positions are unknown today. When depleted each quarry was immediately refilled and recultivated with the excavated material of a new adjacent quarry (so called “Wandernde Brüche”) for the sake of agriculture to go on.

**Diagnosis.** – Body ellipsoidal to circular in outline, rostral and ventral borders of the operculum forming an obtuse angle of 100° to 120°, caudal margin of scales serrated, anterior scales behind the operculum of the second to fourth vertical row with a length/height ratio ranging between 0.29 and 0.32, marginal teeth unicuspid.

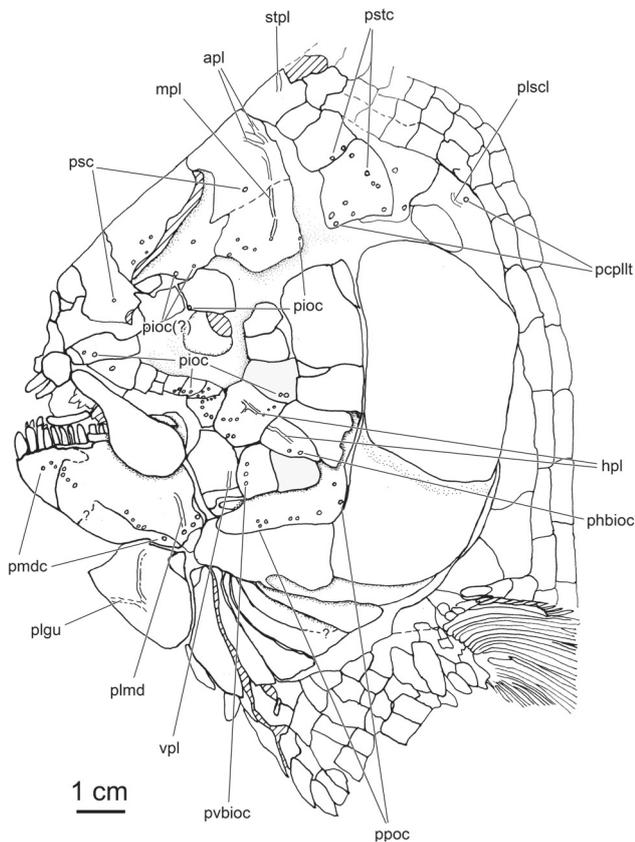
**Remarks.** – None of the characters listed above is apomorphic and the diagnosis is therefore only tentative. The characters are, however, useful in separating *D. stollorum* n. sp. from other Upper Liassic species of *Dapedium*. *D. pholidotum* is also very deep-bodied and has very high and short scales but these are not serrated. *D. caelatum* is more fusiform and shows much more depressed anterior scales. The scales in general are also not serrated in *D. caelatum*.

**Stratigraphical range:** Early Jurassic, Early Toarcian, Tenuicostatum to Bifrons Zone, horizons “Fleins” to “Wilder Schiefer” (Lias  $\epsilon$  II<sub>3</sub> to III).

**Description of the holotype.** – The specimen is a complete fish of 345 mm standard length (from the tip of the snout to the end of the caudal musculature, Pl. 1). The slab containing the specimen is fractured with the fracture cutting through the trunk of the fish from the middle of the back to the middle of the anal fin. The specimen is embedded laterally in clayey sediment with its left side now prepared and observable.

The cranial skeleton is slightly decomposed. Nearly all of the cranial bones are preserved. The dermal cranial ossifications still show their natural arrangement. Some





**Fig. 2.** *Dapedium stollorum* n. sp., holotype, SMNS 16219; pores of sensory canals and pit lines on the cephalic and pectoral girdle skeleton.

dermosphenotic, the supraorbital and the antorbital (Fig. 1, Dsp, Spo, Ant) with the antorbital contacting infraorbital 1. Ventrally and caudally the dermal cover of the cheek is formed by six suborbital plates of varying shape (Fig. 1, So). As in the infraorbitals, fragmentation affects the two largest elements in the series (suborbital 6 = most dorsal suborbital, and suborbital 4 in the ventrocaudal corner of the suborbital series). Fusion of the infraorbitals and suborbitals cannot be observed in the holotype.

The infraorbitals and suborbitals bear an ornament of smaller ganoin tubercles. On the dermosphenotic, supraorbital and antorbital this ornament is developed more coarsely and spaced more densely (Fig. 1).

Pores on the infraorbitals, dermosphenotic and antorbital (Fig. 2, pioc) indicate the presence of canals in these bones for the infraorbital sensory line. Additional pores on the suborbitals 2 and 4 belong to the vertical and horizontal branch, respectively, of the infraorbital canal (Fig. 2, pvbioc, phbioc). On the surface of infraorbital 8 and suborbital 4 run two segments of the horizontal pit line of the cheek (Fig. 2, hpl). A short section of the vertical pit line of the cheek is present on the anteriormost suborbital (suborbital 1; Fig. 2, vpl).

Parasphenoid and vomer. Remains of these bones could not be identified on the holotype.

Jaws. The structure of the dermal skeleton of the jaw apparatus as well as the shape of its individual ossifications are shown in Fig. 1. The following ossifications participate in the formation of the lateral cover of the upper and lower jaw: premaxilla, maxilla, supramaxilla, dentary, splenial, and a compound ossification containing the angular and supraangular (Fig. 1, Pmx, Mx, Smx, De, Spl, Sang+Ang). The anterior suture between the splenial and the co-ossified supraangular and angular is obscured by the ornamentation of these bones. The holotype also shows some medial dermal jaw bones. These comprise the dermopalatinum in the upper jaw and two coronoids in the lower jaw (Fig. 1, Dpal, Co1, Co2). Further medial dermal jaw elements are not visible on the holotype.

Premaxilla, dermopalatine, dentary and the coronoids bear robust marginal teeth (Fig. 3). Exact counts of teeth are impossible due to insufficient preservation and/or partial overlap of the bones concerned by other bones. The premaxilla seems to bear three, the dentary four and the coronoid 1 five marginal teeth. These are styliform and unicuspid and increase in size anteriorly so that the largest teeth found on the premaxilla and dentary measure approximately five millimetres in height.

The outer surface of the premaxilla, maxilla, dentary, supraangular/angular and splenial is ornamented with ganoin tubercles. These are coarsest on the premaxilla and dentary. The articular surface on the dorsal portion of the supraangular/angular for the maxilla is smooth.



**Fig. 3.** *Dapedium stollorum* n. sp., holotype, SMNS 16219; jaw showing unicuspid marginal teeth (photo courtesy by R. BÖTTCHER).

Endochondral jaw ossifications are mostly hidden underneath the dermal cover. A portion of the autopalatine becomes visible in the gap between the maxilla and the infraorbitals (Fig. 1, Apal). The joint between the lower jaw and the palatoquadrate is formed by the articular and the condyle of the quadrate (Fig. 1, Art, pQu). This articulation is strengthened by the quadratojugal (Fig. 1, Quj).

The mandibular sensory canal reaches from the hinder border of the supraangular/angular to the dentary anteriorly as being indicated by pores opening on these bones and the splenial ventrally (Fig. 2, pmdc). The sensory line system on the lower jaw is completed by a vertical mandibular pit line on the posterior surface of the supraangular/angular (Fig. 2, plmd).

**Opercular apparatus.** The opercular apparatus is formed by the operculum, suboperculum, interoperculum, seven branchiostegal rays and a median gular. These ossifications are arranged in a boomerang-shaped series (Fig. 1, Op, Sop, Iop, Rb 1–7, Gu). The corner of this series is filled by the anterior branch of the preoperculum (Fig. 1, Pop). Operculum, suboperculum, interoperculum and gular are shield-like ossifications of varying shape. A distinctive character of the operculum is given by the rostral and ventral borders of the bone meeting at an obtuse angle of about 120°.

All bones of the opercular apparatus bear an ornament of ganoine tubercles. On some bones (Sop, Iop, Pop, some Br) most or all of this ornamentation was destroyed by improper preparation. Tuberculation is denser on the anteroventral bones of the series (Gu, anterior Br) than on the operculum.

Sensory lines are developed on the preoperculum and on the gular. The preopercular canal traverses the horizontal branch of the preoperculum and opens as a series of pores lined up along the posterior and ventral margin of this bone (Fig. 2, ppoc). The gular plate shows a Y-shaped pit line (Fig. 2, plGu).

**Hyoid arch.** The elements of the hyoid arch are hidden underneath superficial dermal bones of the cheek and opercular apparatus and are not visible on the holotype.

**Axial skeleton.** Remains of the axial skeleton are concealed underneath the squamation in the holotype and cannot be observed.

**Pectoral girdle and fin.** Endochondral elements of the pectoral girdle and fin are not visible in the holotype. The dermal shoulder girdle comprises the posttemporal, presupracleithrum, supracleithrum, cleithrum and three postcleithra (Fig. 1, Pstt, Pscl, Scl, Cl, Pcl). Dorsally the girdle is in contact with the neck where the posttemporal touches the two lateral extrascapulars with its long anterior border. It appears in the holotype as if the two lateral extrascapulars have shifted a little over the anterior portion of the posttemporal by post-mortem processes. The presupracleithrum is of oval shape and fills a gap between the posttemporal, supracleithrum and operculum. Three postcleithra

are present in the holotype. These differ from the anterior scales in shape and size. The dorsal and ventral postcleithra are wedge-shaped with the most dorsal one being two and a half times as high as the neighbouring anterior scales. The middle postcleithrum is irregular in outline.

The supracleithrum bears a short curved pit line and a single pore of the canal for the cephalic portion of the lateral line (Fig. 2, plscl, pcpllt). The posttemporal, presupracleithrum and supracleithrum bear an ornament of ganoine tubercles. No ornament is discernable on the outer surface of the cleithrum. This may be because the bone is mostly covered by the operculum and suboperculum.

The pectoral fin is protected by a series of at least 42 fulcra at its anterior edge. At least 18 lepidotrichia are preserved on the left pectoral fin of the holotype. These bifurcate at least two times. The exact number of lepidotrichia cannot be reconstructed in the holotype because of insufficient preservation of the pectoral fin.

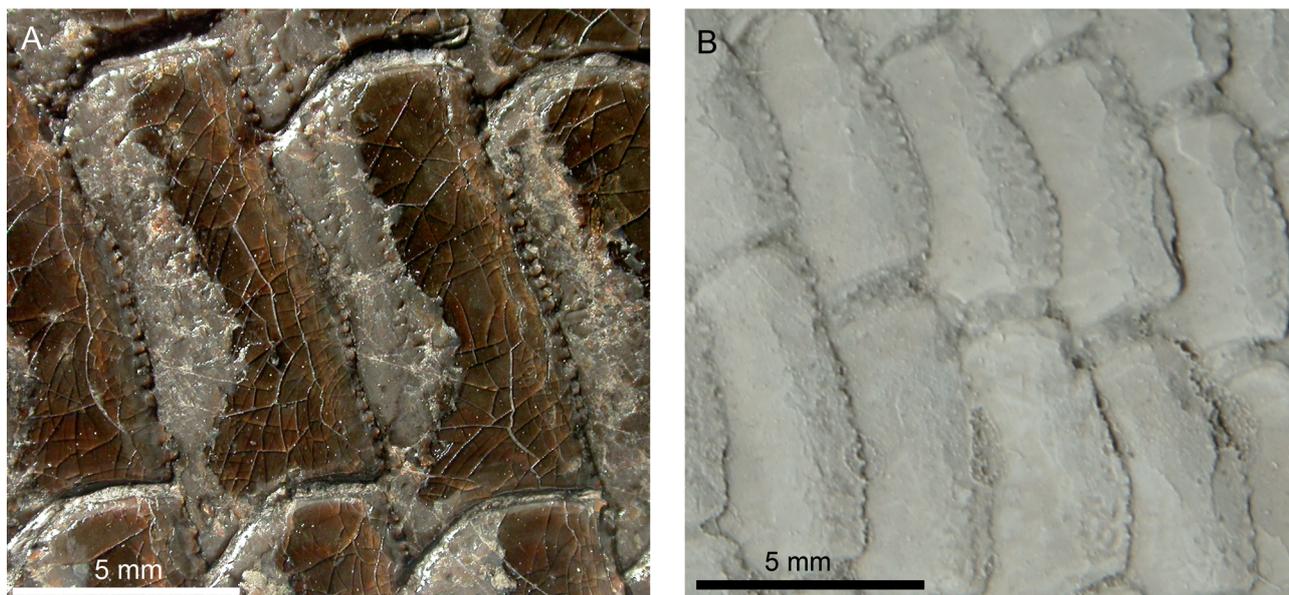
**Pelvic girdle and fin.** The pelvic girdle is obscured in the holotype. The pelvic fin is delicate and much smaller than the pectoral fin. It is supported by at least four branching lepidotrichia of which the third is longest. The anterior edge of the fin is sheltered by a series of at least 22 fulcra. The pelvic fin inserts between the 9<sup>th</sup> and 10<sup>th</sup> vertical rows of scales (Pl. 1).

**Unpaired fins.** The endoskeletal fin support of all fins is covered by scales and is not visible.

**Dorsal fin.** The seam-like dorsal fin is completely preserved (Pl. 1). It reaches from a little behind the middle of the back to the beginning of the caudal peduncle and comprises 24 lepidotrichia that decrease in height posteriorly. The lepidotrichia consist of a long basal segment which continues distally with a series of short segments that bifurcate at least two times. The anterior edge of the fin is protected by a series of fulcra which is only partly preserved. The number of the vertical scale row above which the dorsal fin inserts anteriorly remains obscure because the caudodorsal part of the scale armour has been disturbed by post-mortem processes.

**Anal fin.** The anal fin is as seam-like as the dorsal fin and is built by 15 lepidotrichia (Pl. 1). It inserts anteriorly below the 24<sup>th</sup> vertical row of scales. The lepidotrichia consist of a series of a relatively long basal segments and much shorter distal segments which all bifurcate distally at least two times. The anterior edge of the anal fin is protected by a series of at least 25 fulcra.

**Caudal fin.** The dermal caudal fin skeleton consists of 24 lepidotrichia (Pl. 1). Of these 22 represent principle lepidotrichia (in the sense of SCHULTZE & ARRATIA 1989). Additionally, there are one dorsal and one ventral procurrent lepidotrichium. All lepidotrichia are strongly segmented. The distal part of the caudal fin is not preserved and, therefore, the number of dichotomies of the principle lepidotrichia remains uncertain. The preserved remains of



**Fig. 4.** *Dapedium stollorum* n. sp., flank scales demonstrating the serration at the caudal scale margin. – **A.** Holotype, SMNS 16219 (photo courtesy by R. BÖTTCHER). **B.** Paratype 3, UHH 19 (dusted with ammonium chloride).

these lepidotrichia dichotomize at least three times. The dorsal and ventral edges of the caudal fin are fringed with at least 50 and 57 fulcra, respectively.

**Scales.** The squamation consists of oblique vertical rows of scales. A complete row reaches from the dorsal to the ventral midline of the trunk. Additionally, there are incomplete rows of scales above and below the shoulder girdle and on the caudal peduncle. The caudal margin of the scales is serrated (Fig. 4A).

Counted along the horizontal axis of the body there are 42 complete vertical rows of scales on the left side of the body with row no. 1 immediately neighbouring the postcleithra. Posteriorly, this armour continues with three incomplete vertical rows on the caudal peduncle. Anteriorly, the scale armour is completed by eight short scale rows below and one row above the shoulder girdle (Pl. 1).

The number of individual scales present in vertical rows varies depending on their position within the scale armour. This number increases posteriorad and reaches a maximum in those vertical rows ending ventrally a little in front of and above the insertion of the anal fin. For example, row no. 9 shows 27 scales whereas row no. 21 comprises 33 scales (Pl. 1).

Scale dimensions and proportions also vary according to their position on the body. In the holotype scale dimensions were measured in four different areas of the scale armour: area 1 lies on the anterodorsal part of the trunk above and a little behind the cleithrum; area 2 is located near the centre of the flank; area 3 contains scales covering the ventral part of the caudal peduncle above the end of the anal fin; and area 4 is placed in the body midline imme-

diately behind the shoulder girdle (Pl. 1). In each of these areas the length and height of four scales were measured and an average length/height ratio was calculated (Tab. 1).

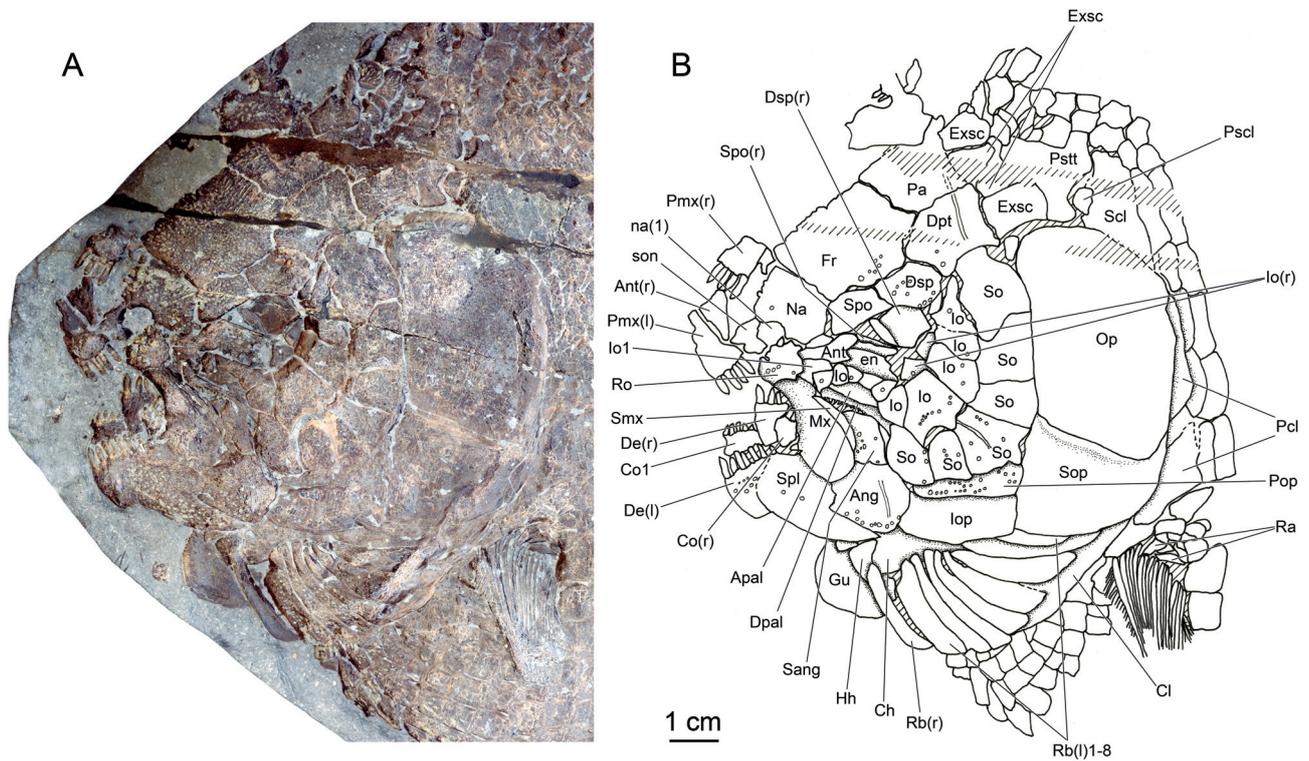
The length of scales was measured as the distance from their posterior border to the posterior border of the foregoing scales parallel to the ventral or dorsal border of the scale concerned. (Because a foregoing scale overlaps the anterior portion of the scale behind to some extent when seen in lateral view, the true length of a scale cannot, of course, be accurately ascertained.) The height of the scales was taken as the distance between the visible dorsal and ventral borders parallel to the posterior rim of the scale concerned.

In area 1, on the anterodorsal part of the trunk, scales are a little more than half as long as high. The average length/height ratio of the four scales considered is 0.58. In area 2, near the centre of the flank, scales are also a little more than half as long as high and come to a mean length/height ratio of 0.61. In area 3, on the caudal peduncle, scales are still less long than high and reach a mean length/height ratio of 0.76. Most conspicuous are scales in area 4 immediately behind the shoulder girdle which are a third as long as high and show a length/height ratio of 0.30.

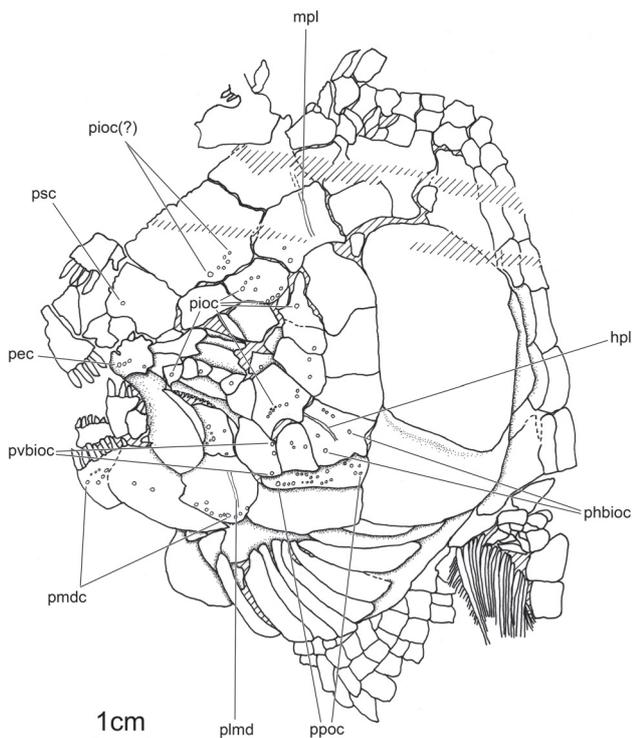
**The paratypes** – additional information and variation.

**Paratype 1** (UHH 3; Figs. 5, 6; Pl. 2). In paratype 1 six instead of four extrascapulars cover the neck region (Fig. 5, Exsc). Also, there are nine suborbitals on the left cheek of paratype 1 (Fig. 5, So). The presupracleithrum is fragmented into two pieces (Fig. 5, Pscl). In the lower jaw





**Fig. 7.** *Dapedium stollorum* n. sp., paratype 2, UHH 35. – A. Head and shoulder girdle in left lateral view. B. Schematic drawing of the cephalic and pectoral girdle skeleton.



**Fig. 8.** *Dapedium stollorum* n. sp., paratype 2, UHH 35; pores of sensory canals and pit lines on the cephalic and pectoral girdle skeleton.

developed as a tabular bone as in the holotype (Fig. 7, Spo). The praemaxillary bears 4 strong styliform, unicuspid teeth (Fig. 7, Pmx). Among all the specimens only in paratype 2 could the rostral be identified with certainty (Fig. 7, Ro) but it does not become clear whether this ossification is paired or unpaired. As shown by pores on its surface, the bone is traversed by the canal for the ethmoidal commissure (Fig. 8, pec). The dermopalatine and the autopalatine become visible in parts but yield only little information on their morphologies except that the dermopalatine bears styliform teeth (Fig. 7, Dpal, Apal). The same applies to the ceratohyal and hypohyal (Fig. 7, Ch, Hh) but both these bones are toothless. As in paratype 1 the splenial takes part in the formation of the dorsal margin of the lower jaw (Fig. 7, Spl). The supraangular is a separate ossification as in paratype 1 but appears to be a little larger than in paratype 1 (Fig. 7, Sang). The supracleithrum lacks a pit line (Fig. 7, Scl). Unlike the holotype and paratype 1, paratype 2 has eight branchiostegal rays (Fig. 7, Br). The number of postcleithra remains obscure but there seem to be only two (Fig. 7, Pcl). The pectoral fin skeleton is supported by rod-like radials (Fig. 7, Ra). The preservation of the scales is poor but some better-preserved scales on the caudal peduncle demonstrate that the scales possess a serrated hinder border. With regard to scale dimensions and proportions, only areas 2 and 4 can be studied in paratype 2. The scales in the positions of areas 1 and 3 are damaged by a fracture in the slab (Pl. 3). The



Agreement also exists in the morphology, dimension and position of the fins (Pls. 1–4). All four specimens are therefore considered as conspecific. Differences in the cephalic ossification architecture, such as fusion or non-fusion of skull roofing and mandibular bones, number and shape of elements in the infraorbital and suborbital series and of the branchiostegal rays as well as fragmentation and fusion of infraorbital and suborbital bones, do not contradict this view. It is known that at least the Upper Liassic *D. pholidotum* shows some intraspecific variability in this respect (WENZ 1968, THIES 1988, THIES & HERZOG 1999). WENZ (1968: 62) mentioned that the ossification pattern of the cheek is subject to intraspecific variability in “holosteans” in general and can be different even in the same individual on both sides of the skull.

#### Comparison with Upper Liassic species from Germany and France

*Dapedium pholidotum* (AGASSIZ, 1832) and *Dapedium caelatum* QUENSTEDT, 1858

As mentioned above, the specimens studied here differ from the contemporaneous *D. pholidotum* and *D. caelatum*, which are also from the *Posidonia* Shale. Differences include body shape, size and scale morphology.

*D. pholidotum* is also of ellipsoidal to circular body shape but remains smaller in size. Adult specimens of *D. pholidotum* (e. g., THIES 1988, pl. 1; HAUFF & HAUFF 1981, fig. 86) measure 170 mm or less in standard length whereas the holotype of the new species reaches 345 mm (Pl. 1). In scale morphology *D. pholidotum* agrees with the specimens described here in regard to proportions. Anterior scales of *D. pholidotum* also show a length/height ratio of about 0.3 (estimated from the specimen in THIES 1988, pl. 1). Scales of *D. pholidotum* disagree, however, with those of the new species in being more delicate and fragile and in having a smooth, unserrated caudal margin (THIES 1988).

*D. caelatum*, on the other hand, is less deep-bodied and fusiform; it is larger than the specimens studied here, having a maximum known standard length of at least 450 mm (estimated from specimen SMNS 56226 in THIES & HERZOG 1999, fig. 1A). The rostral and ventral borders of the operculum pass into one another and together take a sinusoidal course in *D. caelatum* whereas they meet at an obtuse angle in the new species (Pls. 7, 1). Also, scales are unserrated in *D. caelatum* and have a length/height ratio in anterior scales in area 4 of 0.50 (Tab. 1, Fig. 10).

It is quite evident from this brief comparison that our specimens do not belong to *D. pholidotum* or *D. caelatum*.

*Dapedium heteroderma* (AGASSIZ, 1832) and *Dapedium ovalis* (AGASSIZ, 1836)

These species are also said to occur in the Upper Liassic of southern Germany but are only poorly known (QUENSTEDT 1858).

*Dapedium heteroderma* (AGASSIZ, 1832) is founded on a fragmentary squamation from the *Posidonia* Shale of southern Germany lacking all fins and a skull that was originally described by AGASSIZ (1832: 147; 1833: 7; 1836a: 206; 1844: tab. 23e, fig. 1) under the name of *Tetragonolepis heteroderma*. The scales are serrated caudally but appear to be even slightly higher proportionally than in our specimens. The fragmentary state of the squamation does not allow exact localisation of scale measurement areas. Comparison with our specimens with regard to scale proportions is therefore difficult. Other diagnostic characters such as body outline and shape of the operculum, however, are not evident from the fossil. The relationships between the specimens studied here and *D. heteroderma* therefore remain obscure. AGASSIZ' specimen belonged to the HARTMANN collection from the early 19<sup>th</sup> century and is possibly lost today (for the fate of that collection see THIES 2008). At least, it is not present in the collection of the Natural History Museum in London (pers. com. Z. JOHANSON). For these reasons we propose considering *Tetragonolepis heteroderma* AGASSIZ, 1832 as a nomen dubium.

*Dapedium ovalis* (AGASSIZ, 1836) was described as *Tetragonolepis ovalis* by AGASSIZ (1836a: 209; 1835b, pl. 21, fig. 3) on specimens from the *Posidonia* Shale of southern Germany. These differ from our specimens in body outline, which is much more elongated, and in having unserrated scales. WOODWARD (1895: 147) and QUENSTEDT (1852: 203) both regarded *D. ovalis* as a ‘variety’ of *D. pholidotum* (AGASSIZ, 1832).

*Dapedium milloti* SAUVAGE, 1891 and *Dapedium magnevillei* (AGASSIZ, 1833)

Further Upper Liassic species of *Dapedium* include *D. milloti* SAUVAGE, 1891 and *D. magnevillei* (AGASSIZ, 1836) from France (WOODWARD 1895). No details of dental morphology and development of the caudal scale margin were given for either *D. milloti* or *D. magnevillei* by SAUVAGE (1891) and AGASSIZ (1836a). Although the holotype of *D. milloti* seems to be badly preserved, the anterior scales behind the operculum are proportionally longer than in our specimens (SAUVAGE 1891, pl. 3). Also, the dermal cephalic bones and the scales lack ornamentation in *D. milloti* (SAUVAGE 1891: 6). The figure of *D. magnevillei* published by AGASSIZ (1835b, pl. 24) shows differently shaped cephalic ossifications in this species. This refers in particular to the opercular bones.

#### “*Dapedium punctatum*” and “*Dapedium leachi*”

QUENSTEDT (1852, 1858) thought that the English Lower Liassic *Dapedium punctatum* AGASSIZ, 1835 also occurred in the Upper Liassic *Posidonia* Shale of south Germany. WOODWARD (1895) characterised the teeth of *D. punctatum* as unicuspid and agreed with QUENSTEDT that this species was present in the Lower Liassic of England and also in the Upper Liassic of south Germany. Since the 19<sup>th</sup>



- the number of at least eight, possibly up to ten infra-orbital bones (only seven of which are preserved) that are not fused to suborbitals (Figs. 1, 10, Io);
- having the largest element of the infraorbital series in the postero-caudal edge of the orbit (Figs. 1, 5, 7, 9, 10, Io);
- possessing an operculum with the rostral and ventral borders forming an angle of ca. 105° (Fig. 10, Op).

More important are, however, the differences in skeletal anatomy. The holotype of *D. punctatum* differs from our *Dapedium* specimens from the Upper Liassic of south Germany by:

- the premaxillary teeth being bicuspid (Fig. 10, Pmx). In *Dapedium stollorum* n. sp. all marginal teeth are unicuspid;
- the dimensions of the anterior scales behind the operculum in the second to fourth vertical row (scales in area 4, Pl. 5) having a length/height ratio of 0.68 (Tab. 1, Fig. 12). In *Dapedium stollorum* n. sp. this value remains much smaller and is only less than the half ranging between 0.29 and 0.32 (Tab. 1, Fig. 12);
- the parietal, frontal and dermopterotic being fused to form a compound bone. In *Dapedium stollorum* n. sp. these bones occur to a varying extent as individual ossifications (Fig. 10, DPF; Figs. 1, 5, 7, 9, Pa, Fr, Dpt);
- an enlarged second anteriormost infraorbital which is two to three times as high as long (Fig. 10, Io). In *Dapedium stollorum* n. sp. this bone remains smaller (Figs. 1, 5, 7, 9, Io);
- having only three extrascapulars on the right side of the neck, with the two lateral extrascapulars being fragmented, showing a rostral and caudal portion each and with the rostral portion being smaller in the most lateral extrascapular (Fig. 10, Exsc). In *Dapedium stollorum* n. sp. are four, unfragmented extrascapulars developed, except in paratype 1, which has even six extrascapulars (Figs. 1, 5, 7, 9, Exsc);
- the dorsal fin being more extended rostrocaudally and being supported by at least 33 lepidotrichia (Pl. 5). In *Dapedium stollorum* n. sp. the dorsal fin comprises less than 30 lepidotrichs (24 in the holotype, 28 in paratype 1; Pls. 1, 2);
- possessing a special ornament on latero-caudal and ventro-caudal cephalic ossifications consisting of scale-like ganoin tubercles (i. e., flattened, dorso-ventrally elongated tubercles with a rounded to semi-circular hinder border bulging caudally). This sort of ornament is most distinct on the dorsal surface of the operculum (Fig. 10, Op). Such an ornament is lacking in *Dapedium stollorum* n. sp.;

- having in general a much coarser and more densely spaced ornament of ganoin tubercles and ridges on the dermal cephalic bones (Fig. 10);
- an orbit being smaller in longitudinal diameter, a feature which is caused by the much enlarged secondmost anterior infraorbital confining the orbit anteriorly (Fig. 10)

This list of differences confirms WAGNER'S (1860) suspicion and leaves no doubt that the specimens of *Dapedium* from the *Posidonia* Shale of south Germany formerly identified as "*D. punctatum*" by QUENSTEDT (1858) and others are not conspecific with *Dapedium punctatum* AGASSIZ, 1835.

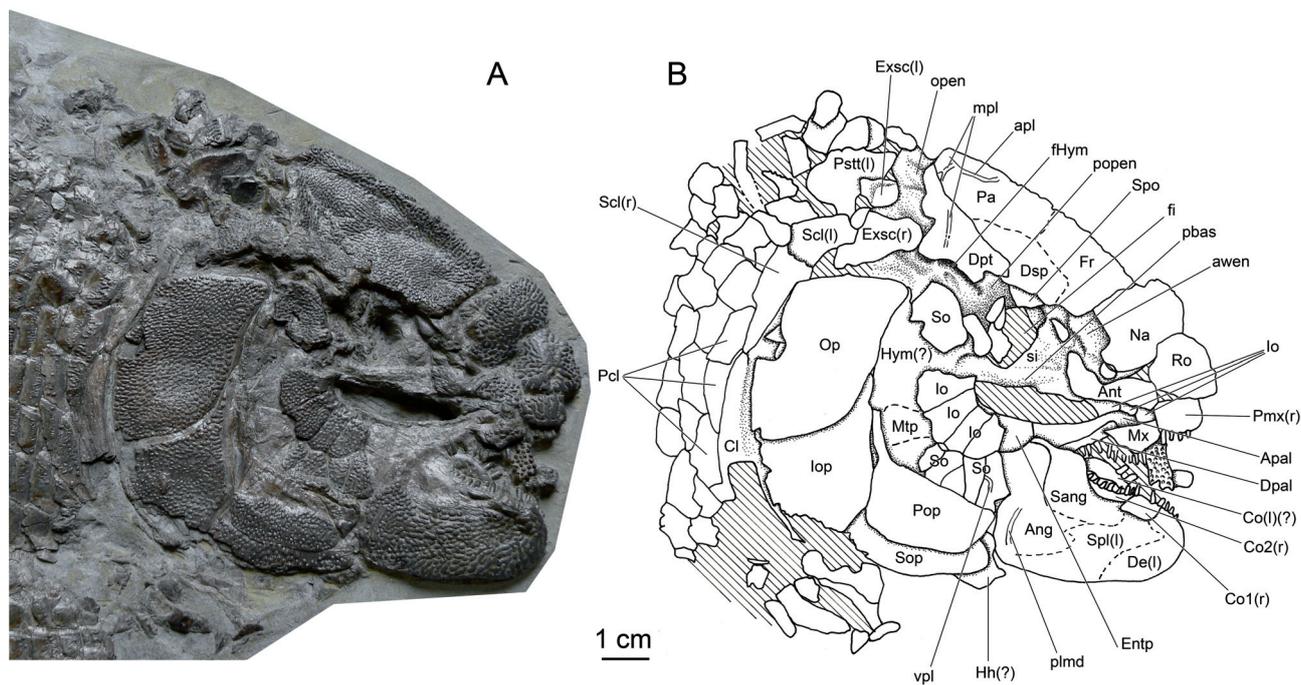
It should also be mentioned that only scales with a smooth hinder margin could be observed on the holotype of *D. punctatum*. The investigation of the specimen was constrained, however, by a thick cover of an unknown protective wax that could not be removed from its surface. Therefore, it cannot be excluded that a caudal serration if present or preserved in some scales was obscured by this thick layer of wax.

#### Further Lower Liassic species of *Dapedium* from England

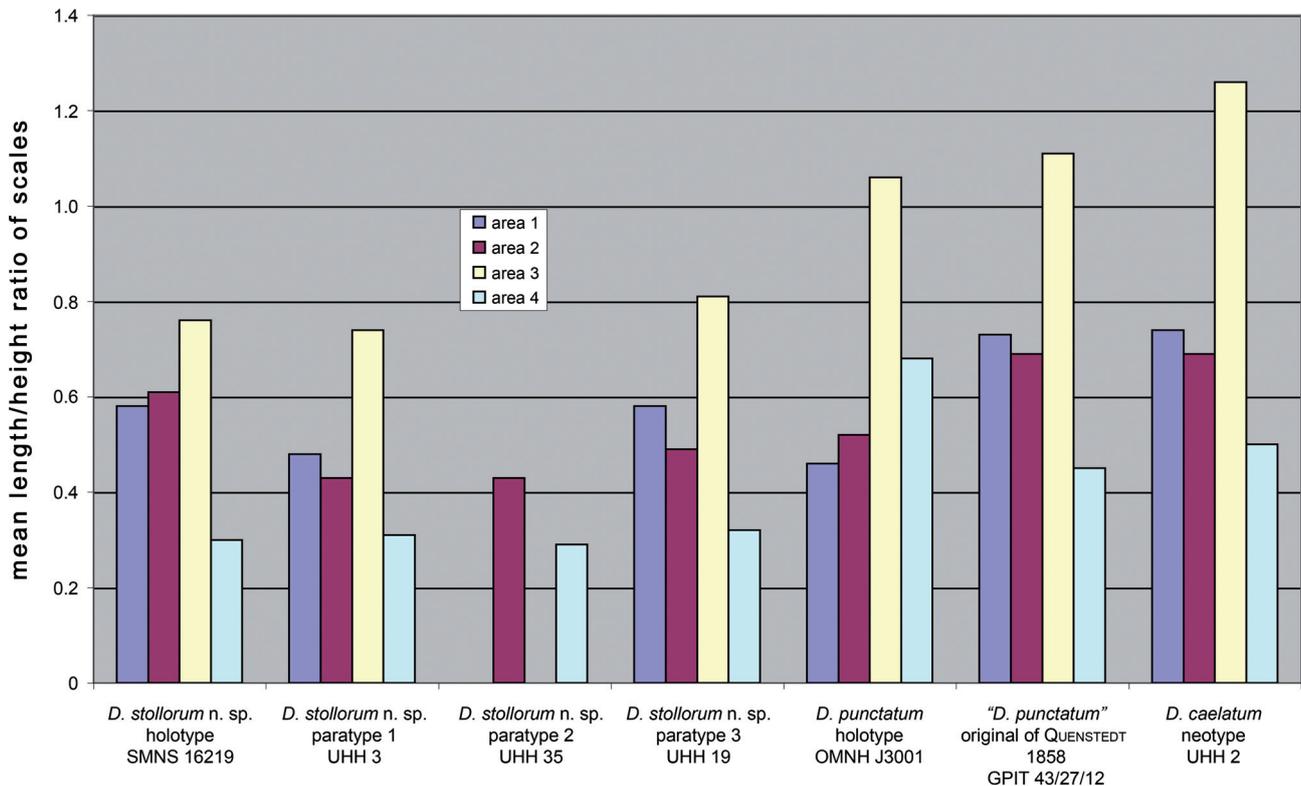
WOODWARD (1895) listed further Lower Liassic species of *Dapedium*: *D. politum* LEACH, 1822, *D. radiatum* (AGASSIZ, 1836), *D. orbis* AGASSIZ, 1836, *D. dorsalis* (AGASSIZ, 1836), *D. colei* AGASSIZ, 1835, and *D. granulatus* AGASSIZ, 1835. All of these species have bicuspid marginal teeth (WOODWARD 1895: 133). WOODWARD (1895) also mentioned *D. angulifer* (AGASSIZ, 1832) from the Lower Liassic of England and even though this species has unicuspid teeth its flank scales are smooth and almost as long as high.

### 3. Results

Superficial resemblance made QUENSTEDT (1858: 226) think that the taxon *Dapedium punctatum* AGASSIZ, 1835 from the Lower Liassic of England was also present among the specimens of *Dapedium* from the *Posidonia* Shale even though he had already noticed that the specimens concerned had unicuspid marginal teeth. By doing so he ignored AGASSIZ' (1835a: 193; 1836b, pl. 25a, pl. 25, fig. 6d) original description and figures of *D. punctatum* explicitly characterising the marginal teeth of this species as bicuspid. QUENSTEDT (1858: pl. 27, figs. 4–12; pl. 28, figs. 3–4; pl. 29, figs. 1–2) figured two specimens of his so-called "*D. punctatum*". The specimen on pl. 27 still exists (GPIT 43/27/12) and was also studied for comparison purposes (Fig. 11, Pl. 6). This comparison reveals that QUENSTEDT'S specimen differs from the four specimens described here in:



**Fig. 11.** “*Dapedium punctatum* AGASSIZ, 1835”, original of QUENSTEDT (1858, pl. 27, figs. 4–12), GPIT 43/27/12. – **A.** Head and shoulder girdle in right lateral view. **B.** Schematic drawing of the cephalic and pectoral girdle skeleton. The specific identity of the specimen is uncertain at present.



**Fig. 12.** Histogram showing mean length/height ratios of scales in the trunk areas 1, 2, 3, and 4 of *Dapedium stollorum* n. sp., *D. punctatum* (Lower Liassic), “*D. punctatum*” (Upper Liassic), and *D. caelatum* (see Pls. 1–7). Values taken from Table 1.

- the dimensions of the anterior scales behind the operculum in the second to fourth vertical row (scales in area 4, Pl. 6) having a length/height ratio of 0.45 compared to values ranging between 0.29 to 0.32 in our specimens (Tab. 1, Fig. 12);
- the scales being smooth instead of serrated caudally;
- the shape of the operculum being curved sinusoidally anteriorly and ventrally instead of having the rostral and ventral borders of the bone forming an obtuse angle (Figs. 1, 5, 7, 9, 11, Op).

From these differences we conclude that QUENSTEDT's and our specimens are not conspecific. The actual specific identity of QUENSTEDT's specimen remains obscure at the moment because it also differs in scale dimensions and proportions from the contemporaneous *D. pholidotum* (THIES 1988). A similar length/height ratio of 0.50 in the anterior scales of area 4 is found, however, in *D. caelatum*, which also has an operculum with a sinusoidally curved rostroventral border (Tab. 1, Fig. 12, Pl. 7). QUENSTEDT's specimen might therefore belong to *D. caelatum* but this assumption needs further investigation and is beyond the scope of this study.

It is evident from the above discussion that the four specimens of *Dapedium* LEACH, 1822 from the Lower Jurassic *Posidonia* Shale of southern Germany do not belong to *D. punctatum* or any other known species of *Dapedium* but represent a different taxon. For this new species we propose here the name *Dapedium stollorum* n. sp.

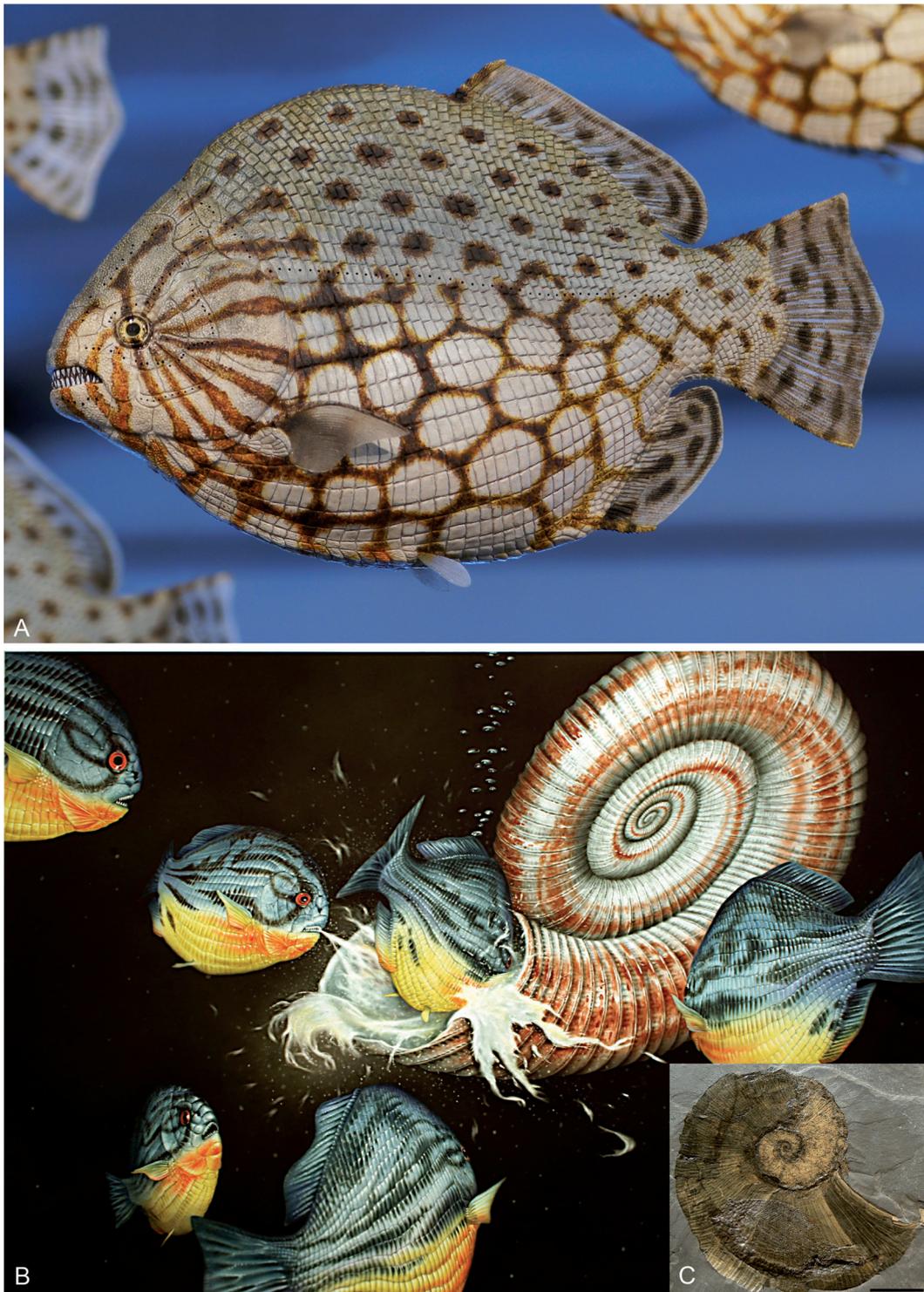
#### 4. Reconstructions of *Dapedium*

*Dapedium* was among the first fossil organisms to be reconstructed by scientists. In 1830 the English geologist and artist H. T. DE LA BECHE painted a watercolour named "Duria Antiquior" (A more ancient Dorset), which in later versions became very famous and popular. This pictorial scene from deep time shows an assemblage of reconstructed fossil marine reptiles and fishes of which the remains had been collected from the Lower Jurassic outcrops at Lyme Regis, England. Among the fossil animals is an unfortunate specimen of *Dapedium* captured at the very moment when it was eaten by an ichthyosaur (RUDWICK 1995).

Later, WOODWARD (1895) included a phenotypical and skeletal reconstruction of *Dapedium* in his "Catalogue of the Fossil Fishes"; this was carried out by GERTRUDE M. WOODWARD according to ARTHUR SMITH WOODWARD's instructions (S. TURNER pers. comm.). WOODWARD's drawings were adopted by subsequent workers such as LEHMAN (1966). Obviously also based on WOODWARD's reconstruction COX et al. (1989) presented in a popular science book on dinosaurs and other prehistoric animals a coloured reconstruction of *Dapedium* as it might have looked during

life. All of these reconstructions are to some extent generalised and schematic and no longer match the results of modern studies of *Dapedium* and subsequent interpretation. Since the Urweltmuseum Hauff in Holzmaden houses the paratypes and further material of *Dapedium stollorum* n. sp., the museum ordered a three-dimensional model of the new species from the German biologist and artist ADAM PROCHÁZKA (Baden-Baden). This model (Fig. 13A), based essentially on specimen UHH 3 (paratype 1), has a total length of 34 cm (as paratype 1). The colouration does not refer to a particular lifestyle of *D. stollorum* n. sp., an attribute which is still unknown for all species of *Dapedium*. The proposed pattern is based to some extent on the Recent Common Scat, *Scatophagus argus* (LINNAEUS, 1766), which is of a similar body shape and size. The openings of the canal pores are coloured in black in order to visualise the system of sensory canals and their course. In life the canals and their pores were certainly filled with mucus as in Recent fishes and were therefore only partially visible.

Additionally, a pictorial reconstruction of the Upper Liassic *Dapedium*, not based on particular specimens, is shown in the Urweltmuseum Hauff as part of a slide show (Fig. 13B). In the picture painted by the German illustrator KNUT MAIBAUM (Hamburg) several specimens of *Dapedium* have gathered to scavenge on an ammonite carcass. Even though the diet of *Dapedium* is still unknown, the only slightly adapted styloform, unicuspid morphology of the teeth of the Upper Liassic representatives of *Dapedium* indicates that it was not specialised for a certain kind of food and so *Dapedium* very probably used different food sources. One can therefore imagine that the Upper Liassic *Dapedium* could well have been feeding on carrion as well as having captured live prey such as molluscs or other invertebrates. A scavenging mode of life is also indicated by a fossil shell of the ammonite *Lytoceras* containing an unidentified specimen of *Dapedium* in its body chamber (Fig. 13C). One may assume that when tearing off parts of the dead cephalopod body one specimen of *Dapedium* was trapped and immobilised inside the body chamber by the stiff and spiny series of fulcra and lepidotrichia at the anterior end of the dorsal and anal fin being hooked in some cephalopod soft parts. After the fish had perished both fossils were buried together. This idea is certainly very speculative but at the moment there is no reasonable alternative explanation for a *Dapedium* being fossilised inside the shell of an ammonite. One can, of course, also assume that the cephalopod ate the fish. This seems, however, very unlikely because of the relatively large size of the fish almost filling the entire body chamber of the shell and because its scale armour is still intact. The fish appears to be too large to have been swallowed whole by the cephalopod. The colouration of the *Dapedium* specimens in Fig. 13B is exaggerated in order to produce a better visual effect but not beyond the range of known reefal fishes.



**Fig. 13.** Reconstructions of *Dapedium*. – **A.** Model of *Dapedium stollorum* n. sp. on exhibition in the Urweltmuseum Hauff, Holzmaden, based on specimen UHH 3 (paratype 1). Total length: 34 cm. **B.** Scene showing a group of *Dapedium* specimens scavenging on a carcass of the ammonite *Lytoceras*. This pictorial reconstruction is part of a slide show presented in the Urweltmuseum Hauff. The reconstruction of the fishes reflects a more generalised view of the life habit of the Upper Liassic *Dapedium*. **C.** Ammonite *Lytoceras* from the *Posidonia* Shale with a specimen of *Dapedium* sp. in the body chamber. The fish possibly became trapped inside the shell when feeding on the carcass of the cephalopod and may therefore indicate that *Dapedium* was an opportunistic carrion feeder (UHH without number); Scale: 5 cm.

**Tab. 1.** Measurements and proportions of scales in different regions of the scale armour of *Dapedium stollorum* n. sp., *Dapedium punctatum* AGASSIZ, 1835, QUENSTEDT's (1858) "*D. punctatum*", and *Dapedium caelatum* QUENSTEDT, 1858. The position of the areas 1, 2, 3 and 4 is shown in Pls. 1–7. The measurements and calculations for the areas 1–3 in the scale armour of *D. caelatum* are taken from THIES et al. (2008). Measurements of scale dimensions were performed on photographs of the specimens concerned applying the computer program "ImageJ" (National Institutes of Health, USA; <http://rsb.info.nih.gov/ij/>).

specimen and scales		length (mm)	height (mm)	l/h ratio	
<i>Dapedium stollorum</i> n. sp. (holotype, SMNS 16219)	area 1	top left	4.7	7.3	0.64
		top right	4.9	7.0	0.70
		bottom left	4.5	9.3	0.48
		bottom right	4.7	9.2	0.51
		<b>mean</b>	<b>4.70</b>	<b>8.20</b>	<b>0.58</b>
	area 2	top left	5.9	9.7	0.61
		top right	6.2	9.7	0.64
		bottom left	6.2	10.8	0.57
		bottom right	6.6	10.9	0.61
		<b>mean</b>	<b>6.23</b>	<b>10.28</b>	<b>0.61</b>
	area 3	top left	3.4	4.3	0.79
		top right	3.7	4.1	0.90
		bottom left	3.8	5.9	0.64
		bottom right	3.8	5.3	0.72
		<b>mean</b>	<b>3.68</b>	<b>4.90</b>	<b>0.76</b>
	area 4	top left	3.9	14.2	0.27
		top right	3.8	13.7	0.28
		bottom left	3.9	13.9	0.28
		bottom right	4.6	12.9	0.36
		<b>mean</b>	<b>4.05</b>	<b>13.68</b>	<b>0.30</b>
<i>Dapedium stollorum</i> n. sp. (paratype 1, UHH 3)	area 1	top left	4.3	7.5	0.57
		top right	3.7	7.2	0.51
		bottom left	4.1	10.1	0.41
		bottom right	4.2	10.3	0.41
		<b>mean</b>	<b>4.08</b>	<b>8.78</b>	<b>0.48</b>
	area 2	top left	3.8	10.6	0.36
		top right	4.3	9.8	0.44
		bottom left	4.8	10.5	0.46
		bottom right	4.7	10.4	0.45
		<b>mean</b>	<b>4.40</b>	<b>10.33</b>	<b>0.43</b>
	area 3	top left	3.3	4.5	0.73
		top right	3.4	4.5	0.76
		bottom left	3.3	4.3	0.77
		bottom right	3.3	4.8	0.69
		<b>mean</b>	<b>3.33</b>	<b>4.53</b>	<b>0.74</b>
	area 4	top left	3.9	13.0	0.30
		top right	3.2	12.3	0.26
		bottom left	4.3	12.2	0.35
		bottom right	3.9	12.1	0.32
		<b>mean</b>	<b>3.83</b>	<b>12.40</b>	<b>0.31</b>

Tab. 1 (continued)

specimen and scales		length (mm)	height (mm)	l/h ratio	
<i>Dapedium stollorum</i> n. sp. (paratype 2, UHH 35)	area 1	top left	no measurements possible		
		top right			
		bottom left			
		bottom right			
		<b>mean</b>			
	area 2	top left	5.7	12.4	0.46
		top right	5.2	10.9	0.48
		bottom left	5.0	12.1	0.41
		bottom right	4.6	12.3	0.37
		<b>mean</b>	<b>5.13</b>	<b>11.93</b>	<b>0.43</b>
	area 3	top left	no measurements possible		
		top right			
		bottom left			
		bottom right			
		<b>mean</b>			
	area 4	top left	4.4	12.7	0.35
		top right	3.8	13.8	0.28
		bottom left	3.5	13.7	0.26
		bottom right	3.3	12.7	0.26
		<b>mean</b>	<b>3.75</b>	<b>13.23</b>	<b>0.29</b>
<i>Dapedium stollorum</i> n. sp. (paratype 3, UHH 19)	area 1	top left	2.3	3.3	0.70
		top right	2.3	3.9	0.59
		bottom left	1.9	3.9	0.49
		bottom right	2.3	4.3	0.53
		<b>mean</b>	<b>2.20</b>	<b>3.85</b>	<b>0.58</b>
	area 2	top left	3.0	6.8	0.44
		top right	3.1	6.4	0.48
		bottom left	3.4	6.1	0.56
		bottom right	2.7	5.9	0.46
		<b>mean</b>	<b>3.05</b>	<b>6.30</b>	<b>0.49</b>
	area 3	top left	2.3	2.4	0.96
		top right	1.7	2.3	0.74
		bottom left	2.1	2.3	0.91
		bottom right	1.4	2.3	0.61
		<b>mean</b>	<b>1.88</b>	<b>2.33</b>	<b>0.81</b>
	area 4	top left	1.9	6.5	0.29
		top right	2.4	6.1	0.39
		bottom left	2.3	7.8	0.29
		bottom right	2.3	7.8	0.29
		<b>mean</b>	<b>2.23</b>	<b>7.05</b>	<b>0.32</b>

Tab. 1 (continued)

specimen and scales		length (mm)	height (mm)	l/h ratio	
<i>Dapedium punctatum</i> AGASSIZ, 1835 (holotype, OMNH J3001)	area 1	top left	5.0	9.4	0.53
		top right	4.5	10.7	0.42
		bottom left	4.3	10.7	0.40
		bottom right	4.8	10.0	0.48
		<b>mean</b>	<b>4.65</b>	<b>10.20</b>	<b>0.46</b>
	area 2	top left	6.0	11.8	0.51
		top right	5.5	11.3	0.49
		bottom left	6.2	10.7	0.58
		bottom right	5.3	11.0	0.48
		<b>mean</b>	<b>5.75</b>	<b>11.20</b>	<b>0.52</b>
	area 3	top left	5.3	5.9	0.90
		top right	6.9	5.7	1.21
		bottom left	5.5	6.0	0.92
		bottom right	7.3	6.0	1.22
		<b>mean</b>	<b>6.25</b>	<b>5.90</b>	<b>1.06</b>
	area 4	top left	5.7	9.6	0.59
		top right	8.1	8.1	1.00
		bottom left	5.8	12.1	0.48
		bottom right	8.0	12.2	0.66
		<b>mean</b>	<b>6.90</b>	<b>10.50</b>	<b>0.68</b>
“ <i>Dapedium punctatum</i> ” (original of QUENSTEDT 1858: pl. 27. figs. 4–12; GPIT 43/27/12)	area 1	top left	5.4	7.1	0.76
		top right	5.2	6.8	0.76
		bottom left	5.2	7.0	0.74
		bottom right	4.8	7.3	0.66
		<b>mean</b>	<b>5.15</b>	<b>7.05</b>	<b>0.73</b>
	area 2 (11 <sup>th</sup> + 12 <sup>th</sup> row)	top left	5.3	7.6	0.70
		top right	5.4	8.0	0.68
		bottom left	5.2	7.9	0.66
		bottom right	5.5	7.7	0.71
		<b>mean</b>	<b>5.35</b>	<b>7.80</b>	<b>0.69</b>
	area 3	top left	5.3	4.8	1.10
		top right	5.0	4.6	1.09
		bottom left	5.3	4.5	1.18
		bottom right	4.8	4.5	1.07
		<b>mean</b>	<b>5.10</b>	<b>4.60</b>	<b>1.11</b>
	area 4	top left	4.7	10.1	0.47
		top right	3.9	9.7	0.40
		bottom left	5.2	9.6	0.54
		bottom right	3.5	9.5	0.37
		<b>mean</b>	<b>4.33</b>	<b>9.73</b>	<b>0.45</b>

Tab. 1 (continued)

specimen and scales		length (mm)	height (mm)	l/h ratio	
<i>Dapedium caelatum</i> QUENSTEDT, 1858 (neotype, UHH 2)	area 1	top left	4.3	6.2	0.69
		top right	4.6	6.0	0.77
		bottom left	4.9	6.5	0.75
		bottom right	4.9	6.6	0.74
		<b>mean</b>	<b>4.68</b>	<b>6.33</b>	<b>0.74</b>
	area 2	top left	5.1	7.6	0.67
		top right	5.7	8.2	0.70
		bottom left	5.6	8.6	0.65
		bottom right	5.9	7.9	0.75
		<b>mean</b>	<b>5.58</b>	<b>8.08</b>	<b>0.69</b>
	area 3	top left	4.6	3.9	1.18
		top right	5.3	4.2	1.26
		bottom left	4.8	3.7	1.30
		bottom right	5.1	4.0	1.28
		<b>mean</b>	<b>4.95</b>	<b>3.95</b>	<b>1.26</b>
	area 4	top left	3.5	8.5	0.41
		top right	4.9	8.7	0.56
		bottom left	3.5	8.6	0.41
		bottom right	5.2	8.6	0.60
		<b>mean</b>	<b>4.28</b>	<b>8.60</b>	<b>0.50</b>

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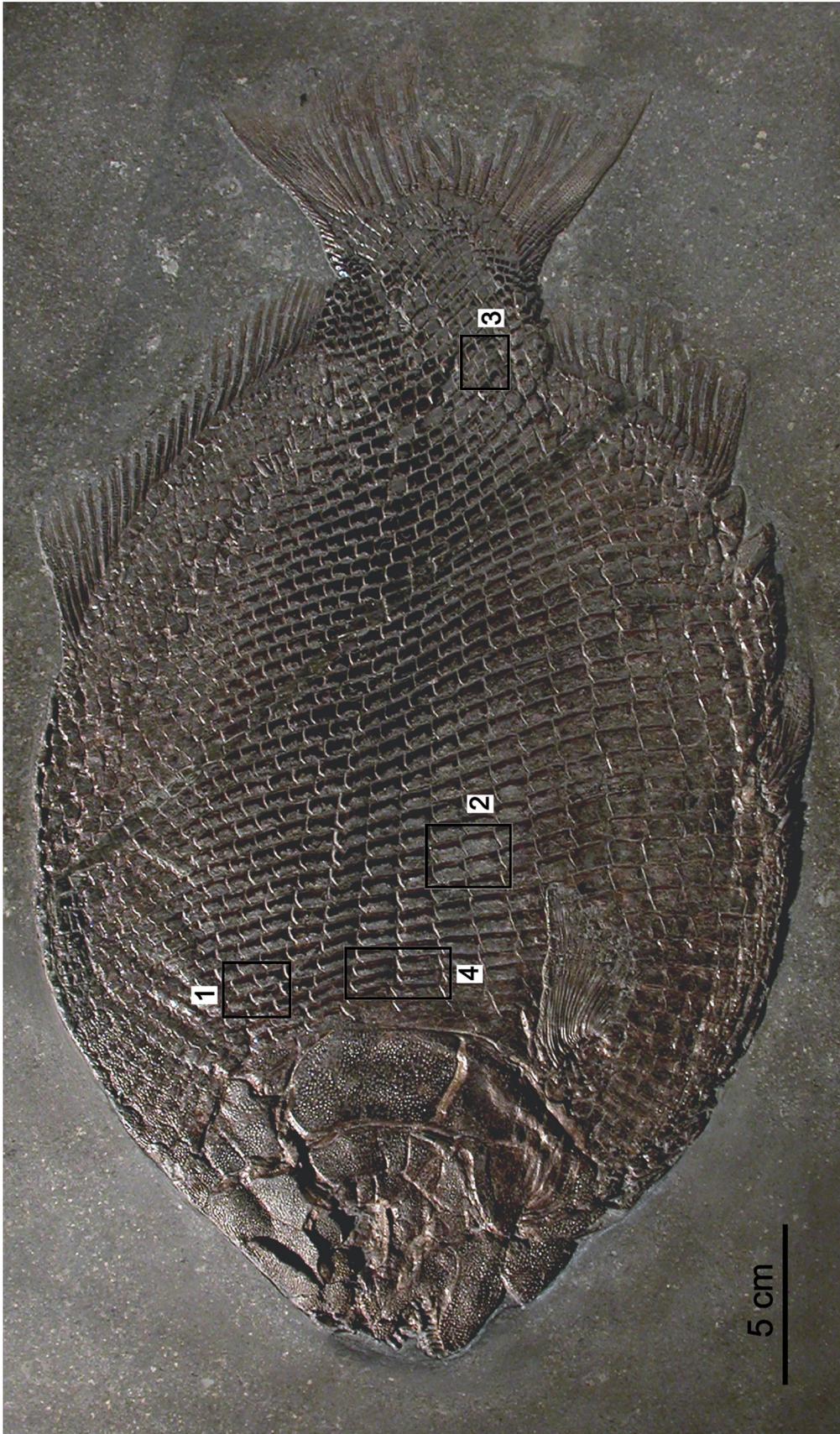
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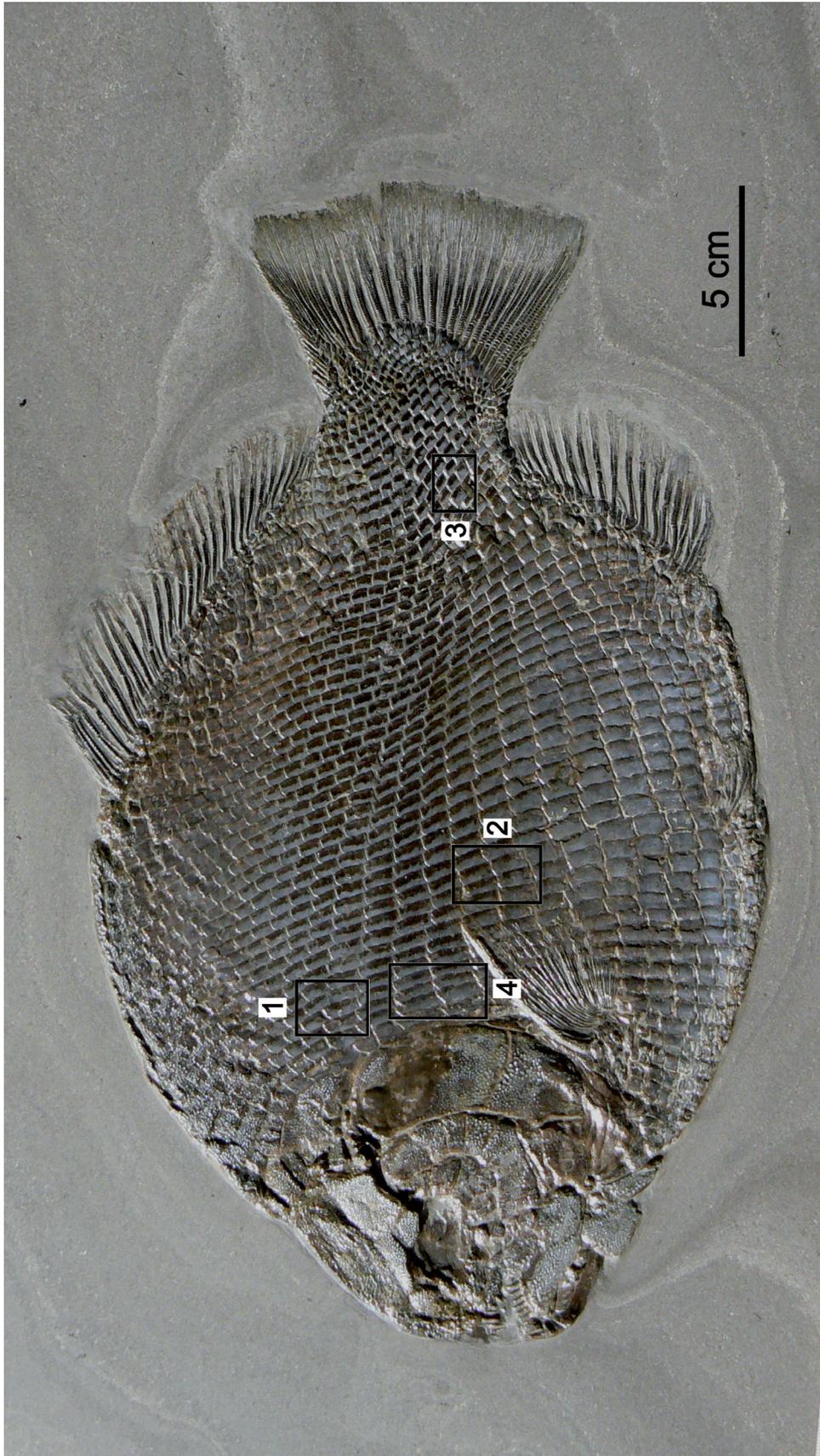
**Plate 1**

*Dapedium stollorum* n. sp., holotype, SMNS 16219; overall view of left lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured (photo courtesy by R. BÖTTCHER).



**Plate 2**

*Dapedium stollorum* n. sp., paratype 1, UHH 3; overall view of left lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured.



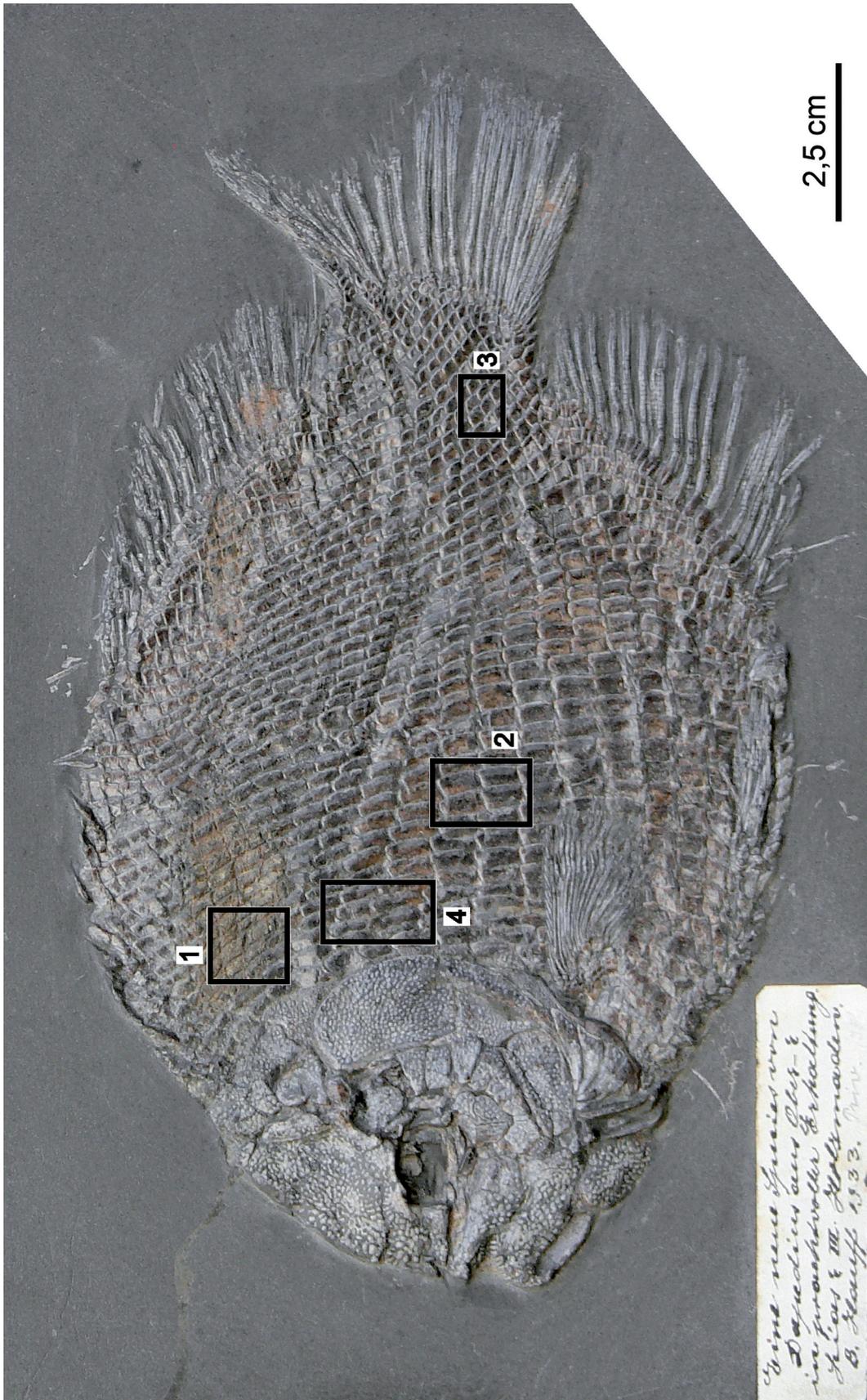
**Plate 3**

*Dapedium stollorum* n. sp., paratype 2, UHH 35; overall view of left lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured.



**Plate 4**

*Dapedium stollorum* n. sp., paratype 3, UHH 19; overall view of left lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured.



2,5 cm

Ein neues Species von  
*Dapedium* aus Ob- &  
im präschotterlichen Erhaltung  
A. Les & M. Hauffen  
B. Hauff 1833. Min.

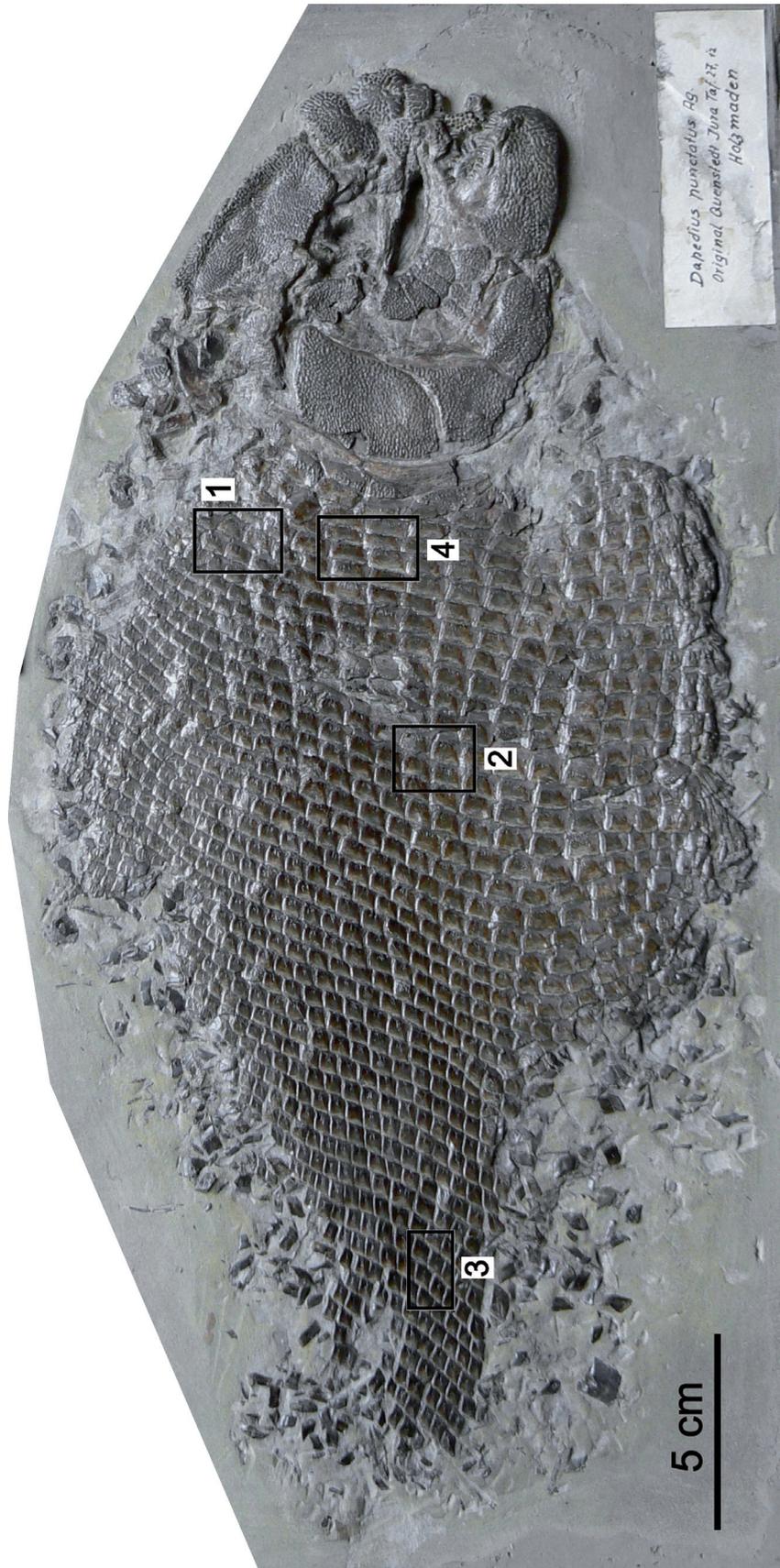
**Plate 5**

*Dapedium punctatum* AGASSIZ, 1835, holotype, OMNH J3001; overall view of right lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured (photo courtesy by P. JEFFERY).



**Plate 6**

“*Dapedium punctatum* AGASSIZ, 1835”, original of QUENSTEDT (1858, pl. 27, figs. 4–12), GPIT 43/27/12; overall view of right lateral side lacking tail and fins except anal fin; squamation partly dissociated possibly by the activities of scavengers; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured. The specific identity of the specimen is unknown at present.



**Plate 7**

*Dapedium caelatum* QUENSTEDT, 1858, neotype, UHH 2; overall view of right lateral side; 1, 2, 3, 4: areas of the scale armour enclosing four chosen scales for each of which the dimensions were measured (after THIES et al. 2008).

