
A new polychelidan lobster from the Alpine Lower Jurassic of southeastern Switzerland

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Abstract :

Polychelidan lobsters are a group of decapod crustaceans which, in terms of both numbers of species and morphology, were more diverse during the Triassic and Jurassic than their modern representatives (Polychelidae). Here a new genus and species from the Lower Jurassic of Switzerland, *Angusteryon oberlii*, is described. The new taxon is characterised by a particularly narrow cephalothoracic shield, which is an unusual trait in comparison to all other polychelidan lobsters, both fossil and extant. It is tentatively assigned to the Coleiidae here. *A. oberlii* nov. gen., nov. sp. was recovered from hemipelagic sedimentary rocks, suggesting that it inhabited a deep-water setting. Although there is a possibility that the present specimens could be parautochthonous, the small size of the ocular incisions may indicate that *A. oberlii* nov. gen., nov. sp. had either reduced vision or was blind, which could be explained by its having inhabited a deep-water habitat. If our views on this mode of life and taxonomic assignment are correct, this would suggest convergent degeneration of vision between the new taxon and the Polychelidae. Furthermore, features of the newly collected specimen augment the apparent morphological diversity displayed by polychelidan lobsters early in their history, as well as document a more substantial decrease of such since the Triassic and Jurassic than previously recorded.

Keywords : Crustacea, Coleiidae, Hettangian, Allgau Formation, palaeobiodiversity, Engadine valley

1. Introduction

Polychelidan lobsters are decapod crustaceans that are characterised by four to five pairs of pereopods that end in claws, a flattened cephalothoracic shield (= carapace), at least in adults and, also in the adult state, a lack of a rostrum, which is replaced by an often concave frontal margin.

Polychelidan lobsters first appeared during the Late Triassic and rapidly became morphologically diverse subsequently. In the 100 million years between the Late Triassic (Carnian, *c.* 230 Ma) and Early Cretaceous (Hauterivian, *c.* 130 Ma), 69 species, in 26 genera, have now been recognised, compared to only 40 extant species, in six genera. Our count of extinct taxa is based AUDO et al. (in press), JAUVION et al. (in press), GAŠPARIČ et al. (this issue); that of extant taxa on GALIL (2000), AHYONG & BROWN (2002), AHYONG & GALIL (2006), AHYONG & CHAN (2008) and ARTÜZ et al. (2014).

Morphologically, modern species differ mainly in the shape of their ocular incisions, epipods and spines (AHYONG 2009; see Fig. 1A-C here), with the notable exception of *Cardus crucifer* (WILLEMOES-SUHM *ex* WYVILLE THOMPSON, 1873) (Fig. 1D). Extinct species display a greater variety, with a wider range in size, including some comparatively large (e.g., *Proeryon giganteus* BEURLIN, 1930 [Fig. 1E], *P. charbonnieri* AUDO & SCHWEIGERT, 2018) and small taxa, or at least those reaching maturity at small sizes, e.g., *Voulteryon parvulus* AUDO, SCHWEIGERT, SAINT MARTIN & CHARBONNIER, 2014b [Fig. 1F]), an unusual cephalothoracic shield shape (rounded in *Cycleryon propinquus* (VON SCHLOTHEIM, 1822) [Fig. 1G], box-like in *Tonneleryon schweigerti* AUDO, 2016 [Fig. 1H], diamond-shaped in *Adamanteryon fourneti* AUDO, SCHWEIGERT, SAINT MARTIN & CHARBONNIER, 2014b [Fig. 1I]) and various strange appendage morphologies, notably pectinate claws in *Palaeopentacheles roettenbacheri* (ZU MÜNSTER, 1839) (Fig. 1J) or frontal lobes in *Knebelia* VAN STRAELEN, 1922 (see Fig. 1K; AUDO et al. 2014a).

Herein, we present yet another oddity among fossil polychelidan lobsters: a new genus and species that is characterised by an extremely narrow cephalothoracic shield, a unique feature.

2. Geography and stratigraphy

The new crustacean material was discovered to the northwest of Piz Chaschauna, on the steep crest between the Trupchun and Chaschauna valleys, near the border of the Swiss National

Park in the upper Engadine valley (Canton Graubünden, southeastern Switzerland; Fig. 2). This region in the south-eastern Swiss Alps is part of the Austroalpine Ortler Nappe, a tectonic unit belonging to a complex of highly allochthonous units of basement rocks and their Mesozoic sedimentary cover in the westernmost part of the Eastern Alps (TRÜMPY 1980; DÖSSEGER 1987; FROITZHEIM et al. 1994; TRÜMPY et al. 1997). The Chaschauna and Trupchun valleys expose a complete section across the northwestern Ortler Nappe, comprising, from south to north, basement gneiss, Permian and Triassic terrestrial detritic sediments, Middle to Upper Triassic shallow-marine carbonates and Lower Jurassic hemipelagic sedimentary rocks (DÖSSEGER et al. 1982; FURRER 1985, 1993). Along the steep crest northwest of Piz Chaschauna, various spectacular exposures display Jurassic and Alpine normal faults (FROITZHEIM 1988). The Upper Triassic strata were reduced in thickness by normal faults and superficial erosion during the Early Jurassic rifting phase (FROITZHEIM & EBERLI 1990). Early Jurassic erosion is documented by chaotic megabreccias that overlie the basal beds of the Upper Triassic Kössen Formation or directly follow on top of the fractured Hauptdolomit (DÖSSEGER et al. 1982; FURRER 1985; for more details, reference is made to SULSER & FURRER 2008).

Stratigraphical sections along the crest northwest of Piz Chaschauna document rapid facies changes in Lower Jurassic strata and variable contacts to the underlying Upper Triassic carbonates (Fig. 3). On the slope southeast of locality P. 2452.8, the Hauptdolomit is reduced in thickness and superficially cut by a system of fissures filled by white dolomitic cement and red dolomitic marlstone. A carbonate breccia and red echinoderm limestone constitute a later fissure filling (Alv breccia, Fig. 3; section A). To the east, a chaotic megabreccia (Chaschauna megabreccia) overlies the truncated basal part of the Norian-Rhaetian Kössen Formation and is characterised by reworked clasts and huge blocks of coral-brachiopod limestones, oolitic limestones and lumachelles from the middle and upper Kössen Formation (Fig. 3; section B). The megabreccia is overlain by calciturbidites and spiculitic limestones (Alpisella beds), followed by a succession of marly limestones and marls with interbedded breccias and calciturbidites (Trupchun beds). Very rare ammonites and belemnites at the base of the Trupchun beds suggest an early Sinemurian age. About 100 m higher up, a succession of marly limestones and marlstones is rich in ammonites of late Sinemurian to earliest Pliensbachian age.

The new lobster material was collected from scree in the small valley of Ils Fouruns between localities P. 2321 and P. 2857 (coordinates: 46°35'24''N/10°03'57''E), together with fragments of penaeid crustaceans and an interesting fauna of dimerelloid brachiopods

(SULSER & FURRER 2008), small crinoid ossicles, pectinoid bivalves, a single gastropod, a fragmentary ammonite (*Waehneroceras?* sp.), several isolated shark teeth (*Sphenodus* sp., *Synechodus pinnai* (DUFFIN, 1987)) and a few disarticulated scales and vertebrae of actinopterygian fish. The fossils are preserved in finely laminated calcareous spiculites without any bioturbation. In addition to dominant sponge spicules (mainly monaxons), a few fragmentary skeletons of dictyid sponges as well as radiolarians and ostracods were found. The same lithology and fauna has been noted in a discontinuous section in the uppermost part of the eastern Ils Fouruns, northwest of locality P. 2857 (Fig. 3; section C, coordinates: 46°35'07''N/10°04'03''E), where the fossiliferous Alpisella beds (10–15 m in thickness) are intercalated between the basal Chaschauna megabreccia and the Trupchun beds. The megabreccia directly covers the upper Hauptdolomit Formation with an angular unconformity. Large olistoliths are also enclosed in the younger Trupchun beds.

The exact age of the Alpisella beds of Ils Fouruns is unknown, in the absence of ammonites and other index fossils. At the base of the overlying Trupchun beds, a single specimen of a Sinemurian ammonite species has been found (*Arnioceras* sp.). Higher up, a succession rich in ammonites of late Sinemurian to earliest Pliensbachian age (*Asteroceras* sp., *Echioceras* sp., *Paltechioceras* sp. and *Uptonia* sp.) is widely distributed across the entire Ortler Nappe (FURRER 1993). In the central Ortler Nappe near Livigno (Il Motto, La Paré), the spiculitic Alpisella beds are overlain by a well-bedded limestone unit (Naira limestone) that has been dated as late Hettangian on ammonite evidence (*Schlotheimia* sp.; FURRER 1985). The most accurately dated section lies in the Alpisella valley north of Monte Torraccia, where an early Hettangian ammonite species, *Psiloceras naumanni* (NEUMAYR, 1879), was recovered from the top of the Alpisella beds, and late Hettangian forms (*Schlotheimia montana* (WÄHNER, 1886) and *Angulaticeras* cf. *marmoreum* (OPPEL, 1862)) were collected from the lower part of the Trupchun beds (CONTI et al. 1994).

3. Material and methods

The present study is based on two specimens from the Lower Jurassic Allgäu Formation that were collected by one of us (HF) and are now housed in the collections of the Palaeontological Institute and Museum, University of Zürich (abbreviation: PIMUZ). The site of Ils Fouruns on the southern flank of Val Trupchun is part of the Swiss National Park and accessible only with a special permit from the Park Board. The fossil crustaceans are

preserved as black exoskeletons, strongly compacted in finely laminated spiculitic limestone. They were prepared mechanically with an air-tool and sharpened needles.

Institutional abbreviations: MNHN.F, Muséum national d'Histoire naturelle (Paris, France), collection of Palaeontology; MNHN.IU, Muséum national d'Histoire naturelle (Paris, France), Collection of Zoology (Crustacea); PIMUZ, Paläontologisches Institut und Museum, Universität Zürich (Zürich, Switzerland); SMNS, Staatliches Museum für Naturkunde (Stuttgart, Germany); SNSB-BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany).

4. Systematic palaeontology

Malacostraca LATREILLE, 1802

Decapoda LATREILLE, 1802

Pleocyemata BURKENROAD, 1963

Polychelida SCHOLTZ & RICHTER, 1995

Eryonoidea DE HAAN, 1841

?Coleiidae VAN STRAELEN, 1925

Genus *Angusteryon* nov.

Type species: *Angusteryon oberlii* nov. sp.

Etymology: Combination of the Latin *angustus*, meaning narrow and *Eryon* DESMAREST, 1817, the first described genus of polychelidan lobsters. Gender: masculine.

Occurrence: Lower Jurassic (Hettangian?), Allgäu Formation (Alpisella beds), Ils Fouruns (community S-chanf, Engadine valley, Canton Graubünden, Switzerland).

Diagnosis: Subrectangular, very elongated and narrow cephalothoracic shield (length more than twice width), tapering gently anteriorly; elongated and narrow pleon, as wide as and

slightly longer than cephalothoracic shield; very elongated P1 merus, almost as long as cephalothoracic shield.

Remarks: *Angusteryon* nov. gen. is considered to be a polychelidan lobster on the basis of its general morphology: the first three pairs of pereopods (thoracopods 4-6) are chelate, and although the diagnostic fourth pereopod (thoracopod 7) is not well preserved, the shape of the first, with a slight concavity on the propodus margin just next to the insertion of the dactylus and the presence of two transverse grooves converging medially, as well as an axial carina on pleonites terga, are typical of polychelidan lobsters. The precise assignment of the new genus within the group is more difficult. The posterolateral angle adjacent to the first pleonite seems to rule out both the Eryonidae DE HAAN, 1841, which show posterolateral angles extending posteriorly but not adjacent to the pleon, and the Polychelidae, which have short posterolateral angles not extending along the whole length of the first pleonite. This leaves two families, namely the Palaeopentachelidae AHYONG, 2009 and Coleiidae. Currently, the Palaeopentachelidae is monotypical, comprising only *Palaeopentacheles roettenbacheri*, which is easily recognised by its pectinate claws. Such claws are absent in *Angusteryon* nov. gen., which would contradict assignment to this family. We therefore tentatively, and by default, assign *Angusteryon* gen. nov. to the diverse Coleiidae.

Angusteryon oberlii nov. gen., nov. sp.

Fig. 4

Coleia viallii; SULSER & FURRER 2008: 208.

Coleia viallii; FURRER 2013: 44, fig. 35.

Etymology: Dedicated to URS OBERLI (St. Gallen, Switzerland), who carefully prepared this unique fossil in 1980, and many others, for HEINZ FURRER between 1979 and 2019.

Holotype: PIMUZ 26673.

Additional specimen: PIMUZ 37364, an isolated claw.

Type locality: Ils Fouruns on the southern side of Val Trupchun (community S-chanf, Engadine valley, Canton Graubünden, eastern Switzerland), part of the Austroalpine Ortler Nappe.

Type horizon: Lower Jurassic (Hettangian?), Allgäu Formation (Alpisella beds).

Occurrence: Currently known only from the type locality.

Diagnosis: See genus.

Description: *Shape of cephalothoracic shield (carapace)* – Cephalothoracic shield subrectangular, tapering anteriorly in outline in ventral view, poorly preserved; frontal margin narrow, possibly concave, poorly preserved; anterolateral angle obtuse and difficult to observe due to preservation; ocular margin poorly preserved, apparently U-shaped; straight anterolateral margin, very slightly oblique compared to the anteroposterior axis; no visible or preserved anterolateral cervical angle near cervical incision; cervical and hepatic incisions hidden by first pereopod; mediolateral margin indistinct; straight posterolateral margin with a few antrorse spines; posterolateral angle quite narrow and extending along s1; posterior margin poorly preserved; sternites not preserved.

Carinae and grooves of cephalothoracic shield – No carinae or grooves preserved.

Pleon and telson – Pleon slightly longer than cephalothoracic shield; first pleonite (s1) poorly preserved; pleonites 2-5 (s2-s5) with two transverse grooves converging medially, the posterior one being cut by the axial carina; sixth pleonite (s6) poorly preserved; telson not preserved.

Eyes and cephalic appendages – Antennula with two long flagella, one of which is approximately the length of the cephalothoracic shield; antenna with endopod forming a long flagellum the entire length of which cannot be observed, but it is longer than the cephalothoracic shield; exopod not preserved; mandible with a long coxal body about one quarter of the cephalothoracic shield in length; maxillae not preserved.

Thoracic appendages – Maxillipeds (thoracopods 1-3) not preserved; first pereopod (P1; thoracopod 4) with a short subtrapezoidal ischium, tapering proximally; P1 merus subrectangular, tapering distally, more than six times as long as ischium, with posterior margin ornamented by small tubercles; P1 carpus subtriangular in outline in ventral view, two times as long as wide, slightly longer than P1 ischium; P1 propodus (including pollex) 1.25

times longer than P1 merus, lateral margin slightly concave just in front of the insertion of the dactylus; P1 pollex (part of propodus opposed to dactylus) straight for most of its length, noticeably curving distally; second pereopod (P2; thoracopod 5) slender and much smaller than P1, ending in a slender claw; third pereopod (P3; thoracopod 6) slender, slightly smaller than P2 and ending in a claw; fourth pereopod (p4; thoracopod 7) slender, poorly preserved; fifth pereopod (P5; thoracopod 8) not preserved.

Pleonal appendages – Male first pleopods forming a copulatory stylet (petasma), long and slender, slightly less than a third of cephalothoracic shield length; other pleopods not preserved.

Ornamentation – Not preserved.

Remarks: The shape of the cephalothorax in *Angusteryon oberlii* nov. gen., nov. sp. is unique among polychelidan lobsters. One possible explanation for this would be that the fossil was secondarily deformed by tectonics, compressed perpendicular to its median axis. Such a deformation is typical of ammonites from the higher part of the Allgäu Formation (Trupchun beds) where the outcrop shows spectacular folds. However, the Alpisella beds, deposited just above the megabreccias are tilted, but not folded blocks of Upper Triassic carbonates and do not show tectonic deformation. The effects of deformation are also absent from brachiopods found in the same beds as the crustaceans (SULSER & FURRER 2008) and in the crustaceans themselves the appendages of the cephalothorax do not appear to have been deformed significantly in any particular direction. Therefore, it is likely that the original shape of the new form is preserved and that it was undoubtedly narrow. Although the margins of the cephalothoracic shield are poorly preserved, several small antrorse spines are observed that often occur on the lateral margin in other polychelidan lobsters, suggesting the margins in this specimen to be complete and not damaged during either the fossilisation process or subsequent preparation.

Angusteryon oberlii nov. gen., nov. sp. was initially identified by one of us (HF) (see SULSER & FURRER 2008) as *Coleia viallii* (see Fig. 4C-E). Indeed, both species share a generally elongated aspect and are not too distant as far as their stratigraphical and geographical ranges are concerned. However, they can be distinguished by several characters:

- the cephalothoracic shield of the new form is much narrower and straighter posteriorly than in *C. viallii*, which is more ovate (Fig. 4C-D);

- lateral margin features of the cephalothoracic shield clearly distinguish both species: *C. viallii* also possesses conspicuous cervical and hepatic incisions of the lateral margin (Fig. 4E; slightly hidden by varnish on the holotype figured in Fig. 4C-D); these are not visible in the new form, but are most likely relatively small;
- the pleon of *A. oberlii* gen. nov., sp. nov. is more elongated, with distinctly longer somites than that of *C. viallii*;
- although the frontal margin of the new form is poorly preserved, it is clearly particularly narrow and cannot therefore have accommodated large eyes such as those of *C. vialli*;
- finally, *A. oberlii* gen. nov., sp. nov. appears to have much longer, thicker antennulae and antenna than *C. viallii*.

5. Discussion

Stratigraphical and sedimentological studies of Lower Jurassic sedimentary rocks in the Austroalpine Ortler Nappe suggest that the fossil lobsters of the Alpisella beds (?Hettangian) are parautochthonous elements that were deposited in a hemipelagic basin by calciturbidites. The associated fauna, rich in brachiopods, siliceous sponges, crinoids and epibenthic bivalves, in addition to the sedimentary facies with megabreccias and turbidites, suggest current-dominated hardgrounds on a submarine high in the northwestern part and deposition along steep fault scarps. Shells and other skeletal elements of dead organisms were transported into the neighbouring basin together with loose sediment. The submarine high was approximately 100 metres below sea level or even deeper, given the total absence of phototrophic organisms such as corals or algae, and the surrounding basin was probably several hundred metres deep (SULSER & FURRER 2008).

Polychelidan lobsters inhabited various palaeoenvironments, not just deep-water settings as many extant species do. Numerous extinct species show well-developed and functional eyes (AUDO et al. 2016). In *A. oberlii* gen. nov., sp. nov., the ocular incisions were rather small (see above) and it is therefore possible that this species had reduced eyes, as was probably also the case in *Tauricheles crymensis* LEVITSKI, 1974 (see AUDO et al. 2018). Reduced eyes and possible reduction or loss of vision would fit well with the environment in which *A. oberlii* gen. nov., sp. nov. was discovered, which was relatively deep and probably well below the euphotic zone. If the assignment of the new form to the Coleiidae is correct, it

would suggest that such degeneration (i.e., reduction or loss of vision) occurred several times among polychelidan lobsters as a group.

The discovery of *Angusteryon oberlii* gen. nov., sp. nov. is another example of the diversity among fossil polychelidan lobsters. It is also the only other polychelidan lobster from the Hettangian with *Wrangelleryon perates* FELDMANN, SCHWEITZER & HAGGART, 2013 and one of the rare polychelidan from extra-alpine Switzerland with the still poorly known “*Eryon*” *escheri* OPPEL, 1862. This diversity suggests that at some point during their evolutionary history, perhaps during the Early Cretaceous when they became extremely rare in the fossil record (GARASSINO et al. 2012; AUDO 2014; AUDO et al. 2018, in press), polychelidan lobsters experienced one or several extinction events. Such events resulted in the survival of only a small number of taxa and greatly reduced their overall diversity. The consequences of these evolutionary bottlenecks are still clearly evident in the modern fauna; with the exception of *Cardus crucifer* (Fig. 1D), all genera of extant polychelidan appear to be closely similar and would probably be placed together if discovered as fossils.

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Captions

Fig. 1. Morphological diversity in polychelidan lobsters. **A–D**, Extant forms (all to scale): *Polycheles typhlops* HELLER, 1862 ♂, MNHN.IU.2014.18022, Mozambique Canal, 460–473 m depth (A); *Stereomastis* sp. ♂, MNHN.IU.2008.10177, Mozambique Canal, 636 m depth (B); *Pentacheles laevis* BATE, 1878 ♂, MNHN.IU.2016.10681, Vanuatu, 700–818 m depth (C); *Cardus crucifer* (WILLEMOES-SUHM *ex* WYVILLE THOMPSON, 1873) ♂, MNHN.IU.2016.8573, Guadeloupe, 270–226 m depth (D). **E–K**, Fossil forms: *Proeryon giganteus* BEURLIN, 1930, unregistered, Urwelt-Museum-Hauff (Holzmaden), Toarcian of Holzmaden (E); *Voulteryon parvulus* AUDO, SCHWEIGERT, SAINT MARTIN & CHARBONNIER, 2014b ♀ (same scale as E), MNHN.F.A50708, Callovian of La Voulte-sur-Rhône (F); *Cycleryon propinquus* (VON SCHLOTHEIM, 1822), MNHN.F.A33518, Tithonian of Eichstätt (G); *Tonnelerion schweigerti* AUDO, 2016, unregistered, Urwelt-Museum-Hauff (Holzmaden), Toarcian of Holzmaden (H); *Adamanterion fourneti* AUDO, SCHWEIGERT, SAINT MARTIN & CHARBONNIER, 2014b, UJF-ID.11541, Callovian of La Voulte-sur-Rhône (I); *Palaeopentacheles roettenbacheri* (ZU MÜNSTER, 1839), SNSB-BSPG AS I 993, Kimmeridgian-Tithonian of Bavaria (J); *Knebelia bilobata* (VON MÜNSTER, 1839), SMNS 70044, Tithonian of Bavaria (K). Scale bars equal 20 mm (A–D, G, H, J, K) and 100 mm (E, F, I). Photographs: Denis Audo (A–F, H–J), Christian Lemzaouda, MNHN (G) and Roger Frattigiani (K).

Fig. 2. Geological map of the area southeast of S-chanf in the Engadine valley, southeastern Switzerland (modified from SULSER & FURRER 2008, with permission of the Swiss Geological Society, November 2019).

Fig. 3. Stratigraphical sections of Upper Triassic and Lower Jurassic strata along the steep crest between Val Trupchun and Val Chaschauna (Ortler Nappe, Austroalpine) (reproduced from SULSER & FURRER 2008, with permission of the Swiss Geological Society, November 2019).

Fig. 4. *Angusteryon oberlii* nov. gen., nov. sp. and *Coleia viallii* PINNA, 1968. A, B, *Angusteryon oberlii* nov. gen., nov. sp. ♂ from the Early Jurassic (Hettangian?) of Ils Fouruns (Switzerland): entire specimen in ventral view (A1) and closeup of spines on the lateral margin (A2) with corresponding interpretative line drawings (B1, B2). C–E, *Coleia viallii* PINNA, 1968 from the Sinemurian of Osteno: part of the holotype under white, cross-polarised light (C) and counterpart in UV autofluorescence (D) with line drawing of the lateral margin from D. Abbreviations: **a1**, antennula; **a2**, antenna; **ca**, carpus; **da**, dactylus; **is**, ischium; **md**, mandible; **me**, merus; P1-P3, pereopod 1-3 (= thoracopod 4-7); **pe**, petasma; **pro**, propodus; s1-s6, pleonite 1-6. Scale bars equal 50 mm (A1, B1, C, D) and 5 mm (A2, B2). Photographs: Rosi Roth (A), Denis Audo (C) and Philippe Loubry, MNHN (D). Line drawings: Denis Audo.

Figure 1

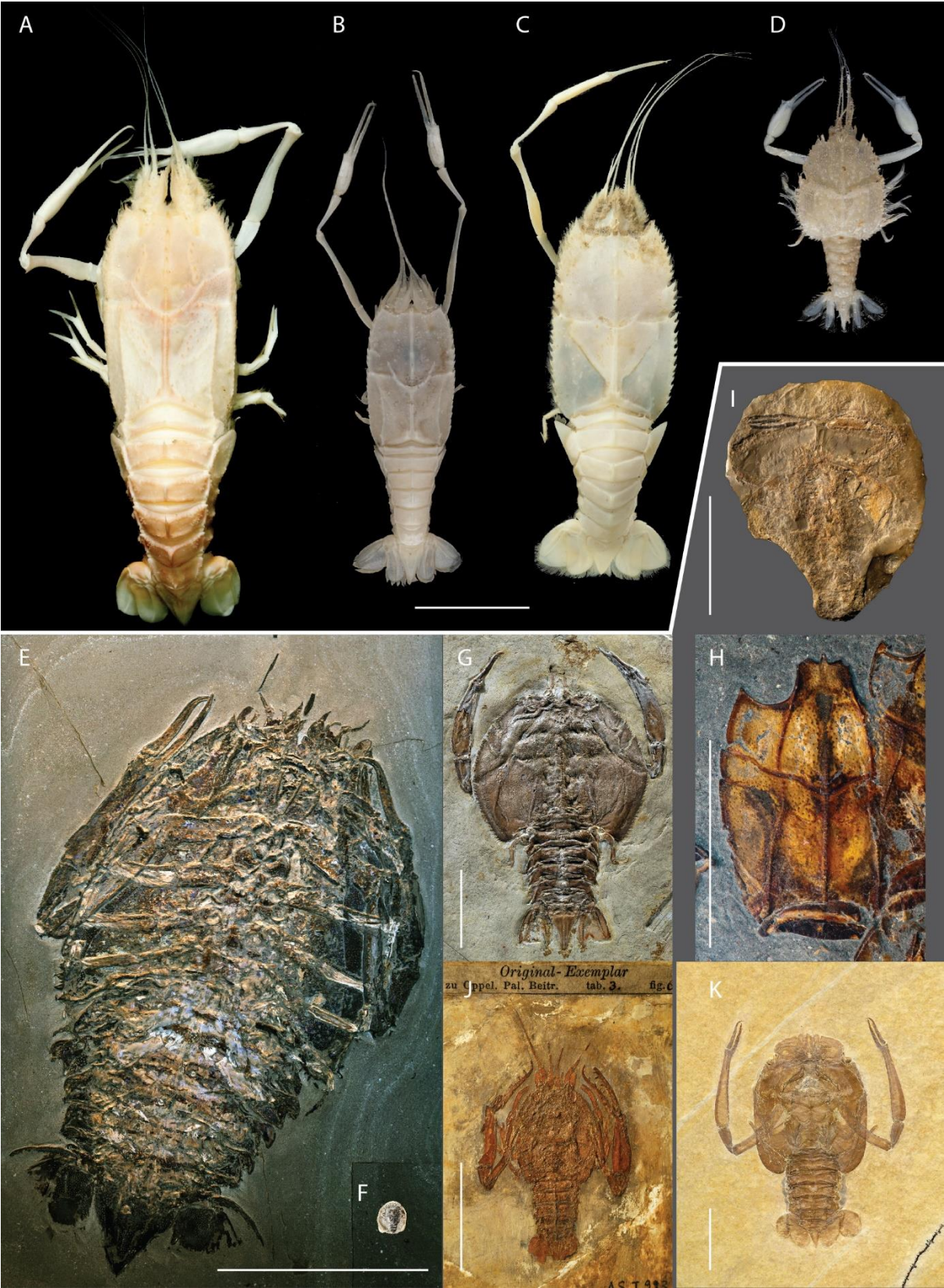


Figure 2

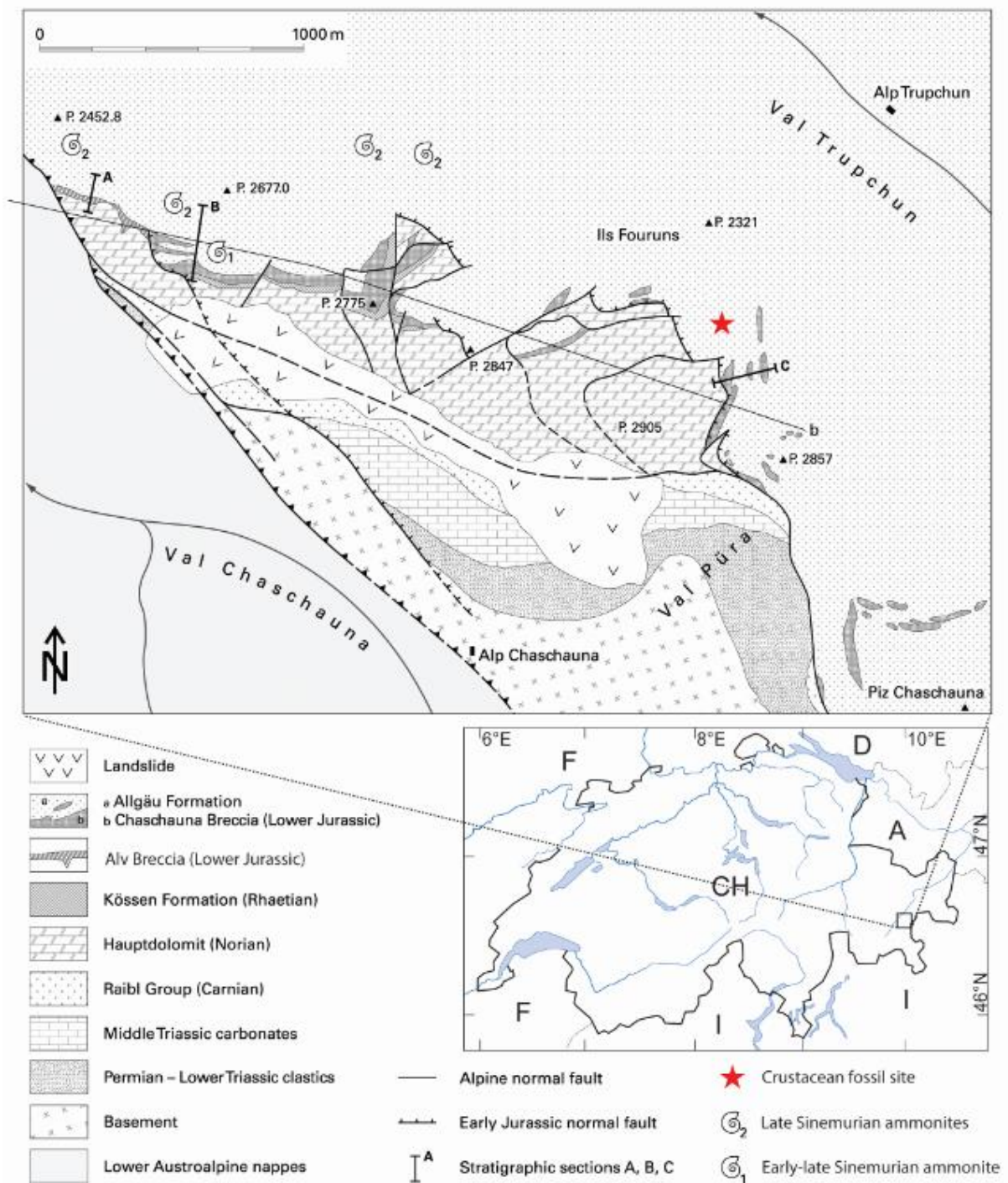


Figure 3

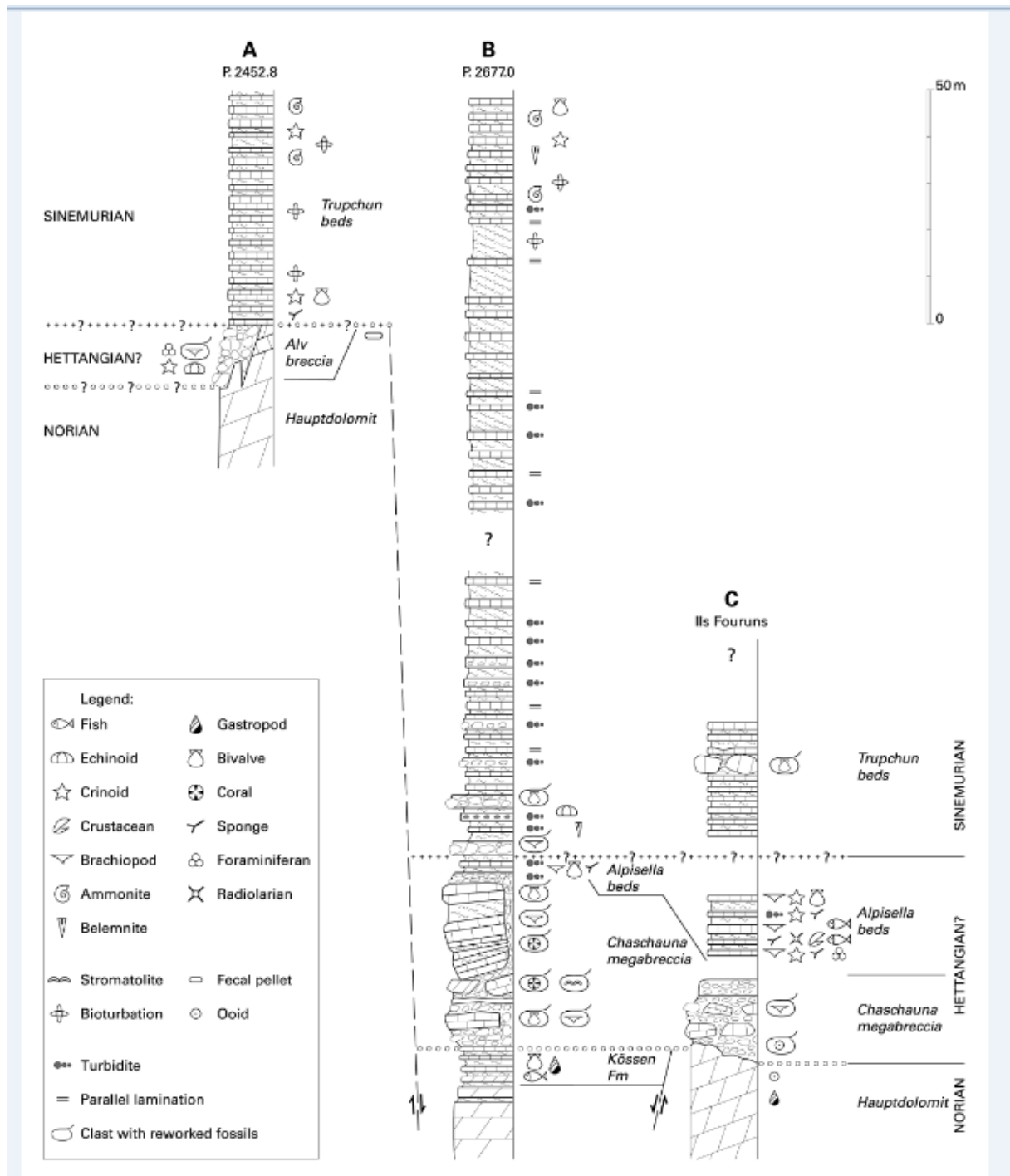


Figure 4

