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RESEARCH ARTICLE

A new pancryptodiran turtle from the Late Jurassic of Poland and palaeobiology of early marine turtles

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Although Western Europe has yielded numerous Jurassic turtle taxa, several represented by cranial material or complete skeletons, the fossil record of the Jurassic turtles remains scarce to the north and east from Germany. Although some Late Jurassic testudinates were historically described from Poland, they were, thus far, represented by fragmentary remains that never were properly figured or described in detail. Therefore, very little is known about the mid-Mesozoic diversity of turtles in that region of the continent. A new pancryptodiran turtle genus and species, *Owadowia borsukbialynickae*, is described from the uppermost Jurassic (Tithonian, ca. 148 Ma) carbonate sediments of the Kcynia Formation in Owadów-Brzezinki Quarry, near Tomaszów Mazowiecki in central Poland. The lower jaw morphology and palaeoecological setting inhabited by the new genus and species, together with the trophic relationships of the Jurassic pancryptodiran turtles, are discussed in an attempt to determine the potential range of mode of life of *O. borsukbialynickae*. We propose that the new specimen belongs to a new durophagous pancryptodiran turtle taxon. *O. borsukbialynickae* might have spent considerable time in the marine environment and specialized on eating hard-shelled invertebrates like bivalves and decapod crustaceans, common to that setting.

KEYWORDS

aquatic turtle, durophagy, lower Tithonian, *Pancryptodira*, Poland, *Testudinata*, Upper Jurassic

1 | INTRODUCTION

Specimens of turtles are rare in the Jurassic fossil record for most of the world, with the exception of several plentiful localities. The uniqueness of the new find of an Upper Jurassic pancryptodiran turtle lies in its very close stratigraphical and geological relationship to one of the most famous Fossil-Lagerstätte localities in the world, Solnhofen-Eichstätt, in southern Germany, where some of the best known and well-preserved taxa of Jurassic turtles have been found (e.g., Gaffney, 1975a, 1975b; Joyce, 2000, 2003; Meyer, 1839a, 1839b, 1860, 1864). Pancryptodiran turtles inhabiting the areas of Solnhofen-Eichstätt (Germany, lower Tithonian) and Owadów-Brzezinki (Poland, uppermost lower Tithonian = middle Volgian) during the Late Jurassic lived under very similar environmental conditions (Błażejowski, Gieszcz, & Tyborowski, 2016). As such, these finds present an unrivalled opportunity for studying their morphology and mode of life. The specimen of a new genus and species, *Owadowia borsukbialynickae*, is the third Late Jurassic occurrence of turtles to be recorded from Poland as well as northeastern Europe. Previously, the only known Jurassic turtle material from Poland comprised fragmentary turtle shells from the Upper Jurassic (Kimmeridgian) of Wrzosowo, Kamień County (Dames, 1888) and Krzyżanowice (Borsuk-Białynicka & Młynarski, 1968). Thus, this discovery of the Upper Jurassic pancryptodiran turtle remains provides valuable data on the geographical distribution of the group. The aim of this paper is to describe a new genus and species, *O. borsukbialynickae*, from the uppermost lower Tithonian Kcynia Formation at the Owadów-Brzezinki Quarry in Central Poland (Figure 1) and assess its paleoecological setting.

2 | GEOLOGY AND TAPHONOMY

The Owadów-Brzezinki Quarry (Figure 1) is located about 18 km southeast of Tomaszów Mazowiecki (Central Poland). Currently, the Owadów-Brzezinki Quarry is the only location in extra-Carpathian Poland where the uppermost lower Tithonian strata are available for study (Kin, Gruszczyński, Martill, Marshall, & Błażejowski, 2013). The palaeontological site located in the Owadów-Brzezinki Quarry is one of the most important palaeontological discoveries described in recent years from Poland, where unusually

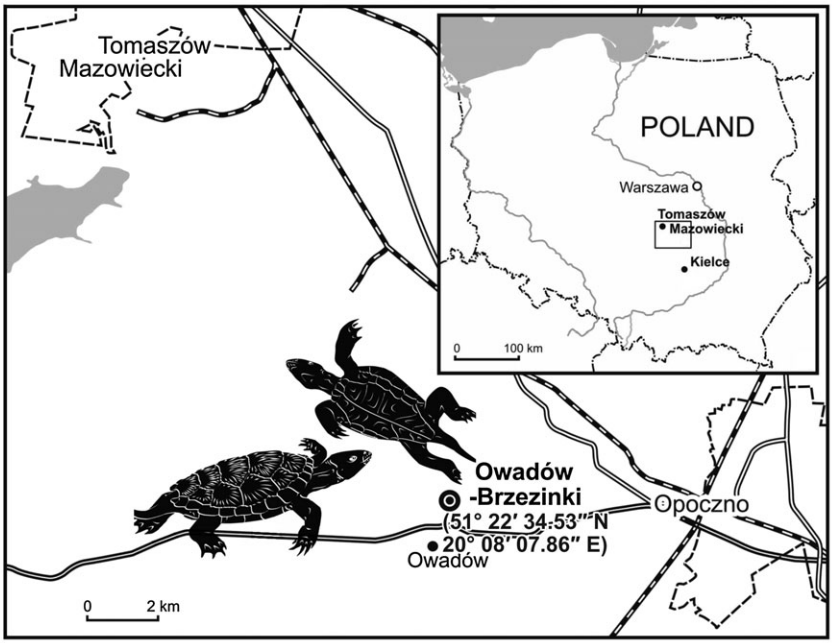

FIGURE 1 The location of the Owadów-Brzezinki Quarry

well-preserved fossils of terrestrial and marine organisms (including ammonites, horseshoe crabs, decapod crustaceans, insects, and remains of various fish and marine reptiles) have been discovered (Błażejowski, 2015; Błażejowski, Gieszcz, Brett, & Binkowski, 2015a; Błażejowski, Lambers, Gieszcz, Tyborowski, & Binkowski, 2015b; Kin & Błażejowski, 2012, 2014; Kin, Błażejowski, & Binkowski, 2012; Kin et al., 2013; Tyborowski, 2017). This assemblage is similar to the famous Solnhofen assemblage from Bavaria, southern Germany (Seilacher, 1970). There are generally many similarities between the Owadów-Brzezinki and Solnhofen region assemblages, which allow for comparative palaeontological studies at a previously unattainable level of taxonomic resolution. The Owadów-Brzezinki Quarry may be regarded as a new "taphonomic window" into the living world of the latest Jurassic, complementing the previously known Fossil-Lagerstätten.

The Upper Jurassic (uppermost lower Tithonian) carbonate sediments of the Kcynia Formation have been subdivided into four distinct lithological units (Błażejowski, Matyja, Wierzbowski, & Wierzbowski, 2014). Unit I (ca. 9.1 m thick) consists of massive, fine-grained, chalky limestone characterized by a general absence of sedimentary structures with occasional distinctive parallel lamination only (Wierzbowski et al., 2016). Deep-burrowing bivalves *Pleuromya* sp. accompanied by oysters *Deltoideum* sp. and trigoniid bivalves, brachiopods, gastropods, ammonites, and crinoids are common, especially in the lower part of this unit (Błażejowski et al., 2016). In this unit, one of the limestone beds forms the bone-bearing horizon (Tyborowski, Błażejowski, & Krystek, 2016). This horizon is highly fossiliferous and is dominated by skeletal remains of ichthyosaurians (*Ichthyopterygia*: *Ichthyosauria*), giant actinopterygian fish (*Actinopterygii*: *Halecomorphi*), and marine crocodylomorphs (*Crocodylomorpha*: *Thalattosuchia*), and it yielded a pancryptodiran turtle (*Testudinata*: *Pancryptodira*). The most frequent vertebrate fossils are ribs and other bones of ichthyosaurs (Tyborowski, 2016). The turtle bones are considerably rare and represented by isolated elements. Taphonomical evidence from the marine vertebrate assemblage of the bone-bearing horizon indicates that the unit should be classified as a Konzentrat-Lagerstätte sensu Seilacher (1970). Remains of the marine reptiles from the Owadów-Brzezinki Quarry illustrate two preservational categories (Tyborowski, 2016):

- Isolated bones and bone fragments,
- Disarticulated partial skeletons.

All of the turtle remains fall into the first preservational category. The taphonomy of the bone-bearing horizon suggests local activity of scavengers and subsequent dissolution of some bones. Amongst bones showing an exceptional mode of preservation, there are remains of a turtle. No obvious evidence for scavenging or predation on the preserved turtle bones is evident. There is no size segregation of the bones in this horizon. The sediments of the bone-bearing horizon represent a record of a shallow sea bay or a lagoon. The proximity of the open sea is indicated by numerous specimens of ammonites of the genera *Zaraiskites* and *Virgatopavlovia* (see Matyja & Wierzbowski, 2016). The uniqueness of this newly discovered bone-bearing horizon lies in its very close environmental and biostratigraphical relationship to one of the famous palaeontological localities in the world, Solnhofen, Eichstätt, and Nusplingen in Bavaria, southern Germany, with approximately 2–5 Myr separating them. The assemblage in this horizon is composed entirely of pelagic taxa; no fresh-water or brackish organisms were found, which may suggest a larger distance to the coastline than in Solnhofen. Succeeding Unit I, Unit II (ca. 2.2 m thick) is represented by thin-bedded micritic limestones, which are underlain and overlain by very thin (2–4 cm) marly beds. Bivalves, ammonites, decapod crustaceans, polychaete tubes, rare crinoids, and marine crocodylomorphs are found in these deposits (cf. Błażejowski et al., 2016; Feldmann, Schweitzer, &

Błażejowski, 2015; Kin et al., 2013). Unit III consists of well-bedded micritic limestones (ca. 12.8 m thick) and is very fossiliferous. Numerous specimens of horseshoe crabs have been found in Unit III in association with an enormously rich assemblage (mass accumulations) of soft-shelled bivalves, the remains of various fish and marine reptiles, rare ammonites, decapod crustaceans, land insects (dragonflies, beetles, and grasshoppers), and isolated pterosaurs' teeth (Błażejowski, 2015; Błażejowski, Lambers, Gieszcz, Tyboroski, & Binkowski, 2015b; Błażejowski et al., 2014; Błażejowski et al., 2016; Kin & Błażejowski, 2012; Kin et al., 2012). The uppermost part of the Owadów-Brzezinki profile is represented by Unit IV (ca. 2.2 m thick), highly weathered and karstified, which is developed as organodetritical limestones rich in small oyster-like bivalves, bryozoans and serpulids (forming small bioherms), and rare ammonites (Matyja & Wierzbowski, 2016). The deposits of this unit most probably belong to the lower part of the so-called "serpulite beds" (Bielecka & Sztejn, 1966; Dembowska, 1979).

In general, the first three units (I, II, and III) appear to represent a continuous transition from an offshore to nearshore, perhaps lagoonal settings, whereas Unit IV shows evidence of a return to more open marine conditions (Błażejowski et al., 2014). Below the Kcynia Formation occur yellow-blue marls and marly limestone of the Pałuki Formation (also Tithonian in age).

3 | MATERIALS AND METHODS

The focus of this study is a collection of four bones (lower jaw, Figure 2; right coracoid, Figure 3; right femur and right ilium, Figure 4) of a pancryptodiran turtle skeleton from the Owadów-Brzezinki Quarry. The bone material originates from the Unit I bone-bearing horizon. The material is well-preserved, revealing numerous details of bone morphology and structure. All fossils have been excavated from one sector of the bone-bearing horizon, and because they were found in an association and represent the same state of preservation, we interpret them as belonging to a single specimen. The pancryptodire bones described herein were collected during fieldwork in the Owadów-Brzezinki Quarry (51°22′34.53″N 20°08′07.86″E) in the summer of 2015. This is the first finding of a turtle from that quarry since the beginning of

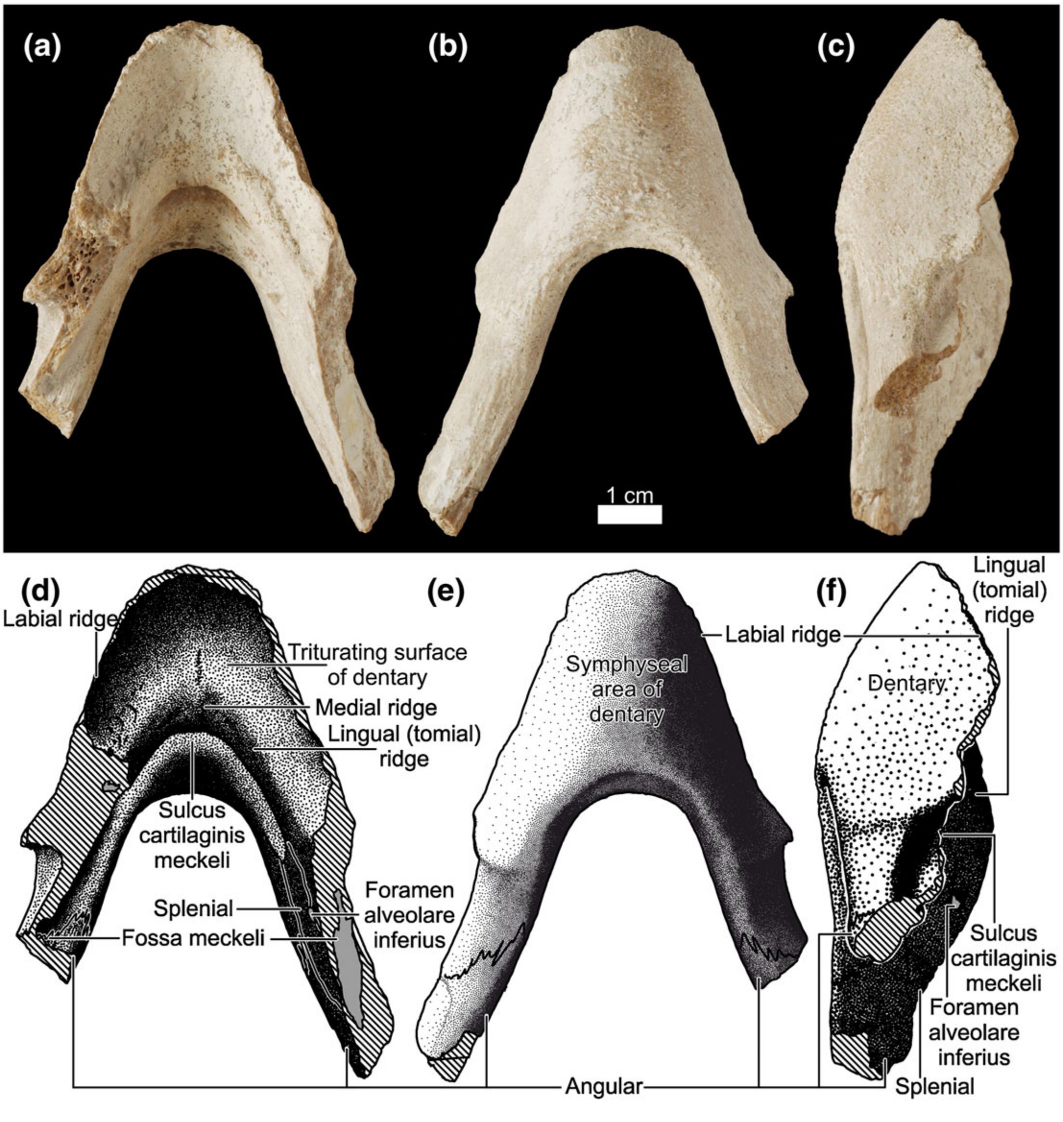

FIGURE 2 ZPAL V/O-B/1959, *Owadowia borsukbialynickae* holotype. Mandible in dorsal (a, d), ventral (b, e), lateral left (c, f) view. Grey is matrix and hatched is broken or damaged bone [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 ZPAL V/O-B/1959, *Owadowia borsukbialynickae* holotype. Right coracoid in lateral (a) dorsal towards left and dorsal (b) view [Colour figure can be viewed at wileyonlinelibrary.com]

its palaeontological exploitation. The collected material is housed in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw.

Institutional abbreviations. ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

4 | SYSTEMATIC PALAEONTOLOGY

Order *Testudinata* Klein, 1760

Pancryptodira Joyce, Parham, & Gauthier, 2004

Incertae sedis

Genus *Owadowia* gen. nov.

Type species. Owadowia borsukbialynickae sp. nov.

Etymology. *Owadowia*, from Owadów-Brzezinki Quarry—the locality where remains of this new turtle were found.

Diagnosis. As for the type and only species.

Owadowia borsukbialynickae sp. nov.

Figures 2–4

Etymology. *borsukbialynickae*, in honour to the Polish palaeontologist, Prof. Magdalena Borsuk-Białynicka—a long time researcher of the Mesozoic reptiles.

Type specimen. ZPAL V/O-B/1959 (Figures 2–4), stored in the collections of the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw, a fragment of the lower jaw, right coracoid, right ilium, and mostly complete right femur.

Type locality. Owadów-Brzezinki Quarry of Nordkalk GmbH, Sławno, close to Tomaszów Mazowiecki (Central Poland); 51°22′34.53″N 20°08′07.86″E.

Occurrence. Kcynia Formation, Tithonian, Upper Jurassic; the first lithofacial unit within *Zaraiskites zarajskensis* subzone.

Diagnosis. Relatively large Jurassic turtle (estimated carapace length around 50 cm) with narrow and V-shaped lower jaw, relatively short and wide but pronounced snout, massive, spoon-like symphysis, no symphyseal hook, well-developed triturating surface in the symphyseal area, moderately developed triturating surface with parallel lingual and labial ridges along the mandibular rami, the labial ridge much higher and sharper than the lingual ridge, the lingual ridge only present laterally and gradually disappearing towards the midline of the symphyseal area, splenial large. The triangular, symmetrical coracoid plate without anterior or posterior expansions, the coracoid neck without coracoid foramen. The slender and proximally and distally slightly curved femur with deep, U-shaped intertrochanteric fossa, small fibular condyle and prominent, well-developed tibial condyle. The ilium with expanded ventral end, constricted neck and well-developed, thin dorsal fan with posterior and no anterior expansion, no signs of sutural attachment to the carapace.

Comparison. Differs from all other Jurassic turtles (including *Plesiochelys* spp., *Portlandemys gracilis*, *Eurysternum wagleri*, *Palaeomedusa testa*, *Jurassichelon oleronensis*, and Jurassic European pleurosternids) but *Solnhofia parsonsi* and *Portlandemys mcdowelli* in more pronounced symphyseal area forming a short snout and lower angle between the mandibular rami. Differs from *S. parsonsi* in broader and more rounded snout, noticeably wider and rounder (instead of narrow angular) posterior edge of the symphyseal area, presence of high labial and low lingual ridges, and U-shaped intertrochanteric fossa. Differs from *S. parsonsi* and *Idiochelys fitzingeri* in larger size. Differs from Plesiochelyidae with the exception of *Portlandemys gracilis* in lower and rounder lingual ridge not reaching the midline of the symphyseal area, narrower distance between the lingual and labial ridges, weaker development of the trough between labial and lingual ridges, no symphyseal hook, and expansion of the triturating surface mostly due to the elongation of the symphyseal area instead of decrease of the distance between lingual ridges. Differs from *Craspedochelys jaccardi* in more expanded ventral portion of the ilium and shorter, not bent posterior process of the dorsal ilial fan. Differs from *Eurysternum wagleri* in shorter, less constricted coracoid neck with no coracoid foramen and proportionally smaller, symmetrical coracoid plate with no anterior or posterior expansions. Differs from *Parachelys eichstaettensis* in less constricted coracoid neck, and symmetrical, proportionally shorter, triangular coracoid plate. Differs from *Tholemys passmorei* and *Plesiochelys etalloni* in narrower, symmetrical coracoid plate and uniform, moderately narrow coracoid neck. Differs from most Late Jurassic plesiochelyids, eurysternids, and thalassemydids (including *Tropidemys langii*, *Enaliochelys chelonia*, *S. parsonsi*, and *I. fitzingeri*) in better development of the articular structures of femur (even in subadults). Differs from *Enaliochelys chelonia* in lower angle of the femoral head. Differs from *Thalassemys hugii* and *Anaphotidemys wittei* in more constricted ilial neck, and a well-developed, thin dorsal fan with large posterior expansion and nearly no anterior expansion, and shorter and thicker coracoid neck. Differs from *Thalassemys hugii* in more expanded ventral portion of ilium. Differs from *Thalassemys bruntrutana* in more gracile ilium with shorter posterior process of the dorsal fan. Differs from *Riodevemys inumbragigas* in laterally flattened ilial neck and slightly smaller, flat dorsal fan with posterior process directed posterodorsally.

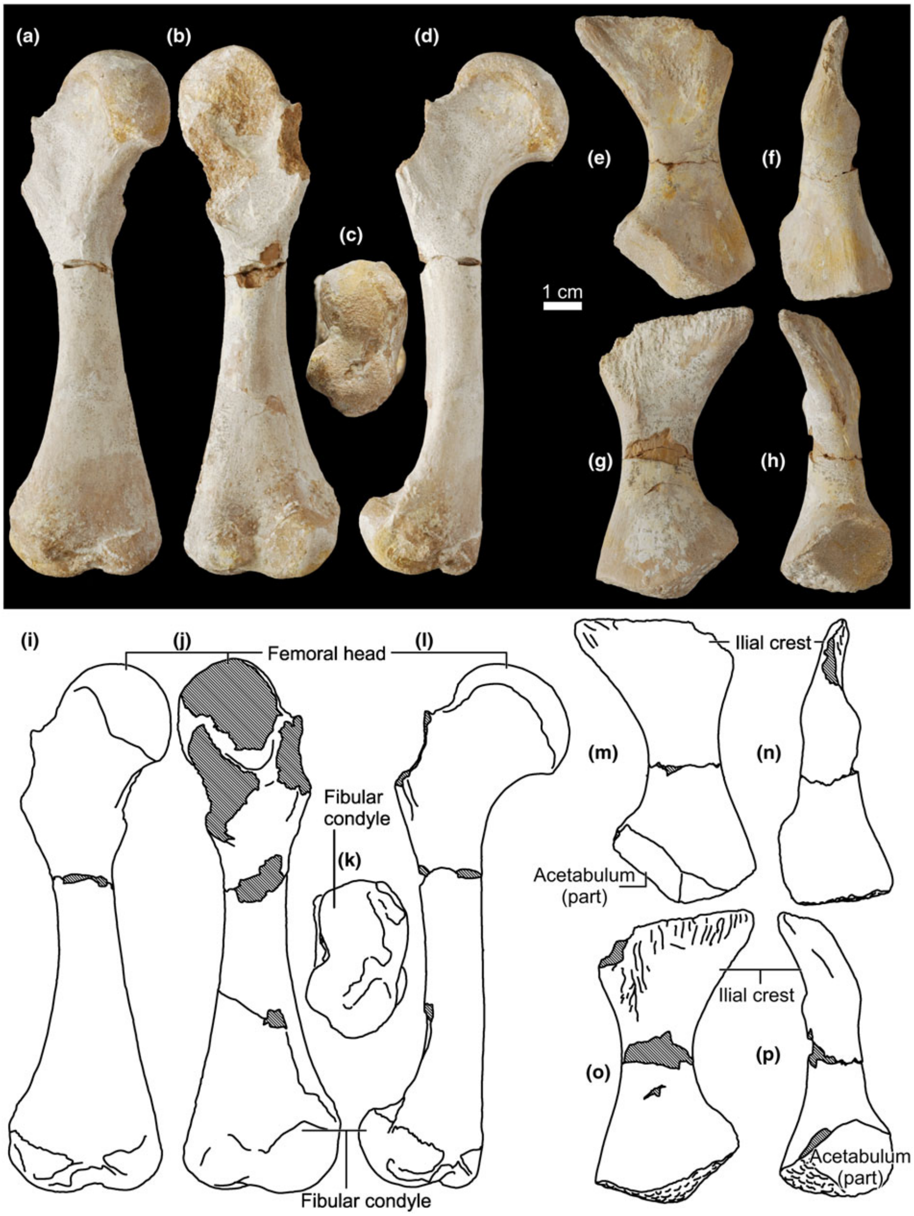

FIGURE 4 ZPAL V/O-B/1959, *Owadowia borsukbialynickae* holotype. Right femur in dorsal (a, i), ventral (b, j), distal (c, k; dorsal towards right), and posterior (d, l) view. Right ilium in lateral (e, m), cranial (f, n), medial (g, o), and caudal (h, p) view. Grey is matrix and hatched is broken or damaged bone [Colour figure can be viewed at wileyonlinelibrary.com]

5 | OSTEOLOGICAL DESCRIPTION

5.1 | Mandible (Figure 2)

Dentary. The lower jaw rami are fused anteriorly into massive and spoon-like symphysis. In dorsal view, the general form of the lower jaw is narrow and V-shaped, rather than broad and U-shaped. Both dentaries are narrow and robust, forming an angle of approximately 35°. The overall length of the conjoined dentaries measured along the midline is 6.6 cm. The left dentary length measured along its long axis is 6.1 cm. The width between the posterior ends of the dentaries is 3.7 cm. The symphysis is similar to that of *S. parsonsi* (Gaffney, 1975b), but it is shorter, wider, and lacks a median trough (Gaffney, 1975b; Joyce, 2000; Parsons & Williams, 1961). The triturating surface of both dentaries is characterized by two parallel labial and lingual (tomial) ridges. Both ridges are well developed, but the lingual ridge is much lower and rounder than the labial ridge. Anteriorly and posteriorly, the labial ridge of the left dentary retains a uniform height. The lingual ridge remains similarly developed for most of its length, but it quickly disappears after reaching the symphyseal area. The labial ridge of the right dentary is damaged posteriorly and a cross-section through the sediment-filled canalis alveolaris inferior can be seen. The triturating surface is relatively robust and narrow with a uniform width of approximately 0.5 cm for most of its length. Unlike in *S. parsonsi* and most plesiochelyids, the expansion of the triturating surface in *O. borsukbialynickae* is attained mainly by elongation of the symphyseal area, and not by decrease of the distance between the lingual ridges (Gaffney, 1975b, 1976; Joyce, 2000; Parsons & Williams, 1961). There is a very gentle, low sagittal crest present on the symphysis; beside which, there are no specific structures present on the symphyseal area.

There is no trace of a symphyseal hook. Posterior part of the symphyseal area is rounded. The sulcus cartilaginis Meckeli is visible in medial view, and it is shallow, broad, and blunt posteriorly, becoming much deeper and narrower anteriorly. Small nutritive foramina are present at the symphysis, which shows that the dentary was covered by a beak. Approximately 1.5 cm behind the caudal end of the symphysis, a low, rugose ridge is present on the lateral surfaces of both dentaries, probably indicating the posterior limit of rhamphotheca. Posteroventrally, the right dentary meets the partial angular. Posteromedially, it meets the splenial.

Angular. The angular of *O. borsukbialynickae* is only partially preserved in posteroventral region of the lower jaw. The bone is visible in ventral, lateral, and medial view. In medial view the dorsoventral extent of its exposition is similar to that in *Plesiochelys etalloni* (Pictet & Humbert, 1857) as figured by Gaffney (1976). Anteriorly, it meets the dentary on the ventral surface of the jaw. The sutural contact between both bones is visible in medial view. Dorsomedially, the angular contacts the preserved splenial. The length of the preserved part of the right angular measured along its long axis is 3 cm.

Splenial. The splenial is only partially present on the right side of the mandible, where it covers the fossa Meckeli medially, similarly like in *Portlandemys mcdowelli* (Gaffney, 1975a), and *Plesiochelys etalloni*, but differently than in *Plesiochelys planiceps* (Owen, 1842), in which the fossa Meckeli is covered by the coronoid (Gaffney, 1976). As in *Plesiochelys etalloni* and differently than in *Portlandemys [or] Po. mcdowelli*, the splenial continues rostrally beyond the dentary-angular suture (Gaffney, 1976). The foramen alveolare inferius is visible at its dorsal border. The splenial as preserved is 3 cm long. There is no splenial present on the left side of the specimen, so the preserved part of the fossa Meckeli is exposed.

5.2 | Pectoral girdle (Figure 3)

Coracoid. A nearly complete right coracoid is present, with only a small fragment of the medial border missing. The proximal part of the coracoid neck is swollen and roughly triangular in cross-section, with a blunt hump on its dorsal side and a rounded lateral edge. Distally, it becomes thinner and flatter and eventually spreads laterally into a triangular, nearly symmetrical flat plate. The neck is slightly curved medially. Both the proximal and the distal ends of the coracoid appear to be nearly undamaged, but their surface is rough, and most likely, they were finished in cartilage, suggesting a subadult age of the specimen. The coracoid is 11 cm long.

5.3 | Pelvic girdle and hindlimb (Figure 4)

Ilium. The right ilium is the only preserved bone of the *O. borsukbialynickae* pelvic girdle. The bone is generally well preserved with the exception of some minor damage to the medial surface of the neck and the anteriormost edge of the dorsal fan. The ilium is morphologically typical for pancryptodiran turtles. The neck is oblate and ellipsoidal in cross-section. The dorsal fan is prominent, well developed, dorsally thin and slightly curved medially, and expanded posteriorly while having nearly no anterior expansion. Its medial side is covered with longitudinal grooves. The ventral part of the ilium is broad and pentagonal in ventral view. The ventral part of the bone is expanded and bears the articular surfaces for the pubis and ischium. The pubic facet is wider than the ischial facet. The pubic and ischial facets are rough, similarly to the scapular facet of the coracoid, suggesting that the articular surface was not fully ossified, possibly due to a young age of the specimen. On the posterior side of the ilium, the dorsal part of the acetabulum is visible. The height of the ilium is 7.5 cm, the breadth at the broadest place in the ventral section is 3 cm in anterior view and 4 cm in lateral view, 1.5 cm at the narrowest point, and the dorsal fan is 4.1 cm long.

Femur. The right femur is well preserved with exception of the major trochanter and the minor trochanter, which are missing, and the ventroanterior part of the femoral head, which is damaged. The length of the femur measured along its long axis is 13.5 cm. The bone is slender and slightly curved on its proximal end and distal end. The shaft of the femur is oval in cross-section at midlength, and gently arched ventrally. In ventral view, between the missing trochanters, the deep and U-shaped intertrochanteric fossa is visible. Although the trochanter major is broken, enough of its base is present to indicate that it was turned ventroanteriorly and separated from the articular surface of the femoral head by a deep notch. The articular surface of the femoral head is prominently rounded and ovoid in dorsal view. The femoral head is set at an angle of approximately 45° relative to the shaft. The breadth of the distal end of the femur is roughly equal to the depth and breadth of the proximal end as preserved. Articular surfaces are well preserved and clearly developed on the ventrodistal end of the femur. The tibial and fibular condyles are prominent, but the tibial condyle is more spherical and larger dorsoventrally than the fibular condyle.

6 | TAXONOMIC IDENTITY OF *OWADOWIA BORSUKBIALYNICKAE*

Most of the bones of *O. borsukbialynickae* are missing, but some comparisons with aquatic pancryptodiran turtles known from Porrentruy, the Solnhofen lithographic limestones, the Solothurn Turtle Limestone, and other European Jurassic localities can be made. Although significant progress was made during the last several decades when it comes to the understanding of the Jurassic turtle diversity, taxonomy, and phylogeny, thanks to the work of several researchers (Anquetin, Deschamps, & Claude, 2014a; Anquetin & Joyce, 2014; Anquetin, Püntener, & Billon-Bruyat, 2014b; Gaffney, 1975a, 1975b; Pérez-García, 2015b, 2015c), still some taxa remain problematic and need revision. The list of specific and generic synonymies compiled by many authors is often impressive and not always mutually compatible. Currently, over 15 species representing at least 12 genera of eurysternids, plesiochelyids, and thalassemydids are considered valid, and still there exist several enigmatic taxa of unresolved taxonomy.

The morphology of the mandible of *O. borsukbialynickae* is distinctive enough to refute its affinity with most of the well-known Late Jurassic turtles. The only Jurassic European pleurosternids with known cranial material, *Pleurosternon bullocki* (Owen, 1842), and *Dorsetochelys delairi* (Evans & Kemp, 1976), seem to have unspecialized mandibles with a short symphyseal area and a symphyseal hook and lack any adaptations of the palate required for durophagy (Evans & Kemp, 1975, 1976). *Pleurosternon bullocki* also differs greatly from *O. borsukbialynickae* in the morphology of the femur and coracoid (Evans & Kemp, 1975). *P. bullocki* and *Riodevemys inumbragigas* (Pérez-García, Royo-Torres, &

Cobos, 2015) also differ from *O. borsukbialynickae* in the morphology of the ilium (Evans & Kemp, 1975; Pérez-García et al., 2015). Furthermore, the turtles belonging to this family are considered to live only in freshwater and are absent from Solnhofen (Pérez-García et al., 2015)—the closest analogue of Owadów-Brzezinki locality. The only Late Jurassic turtles with known lower jaws that have an elongated symphyseal area are *P. mcdowelli* (Plesiochelyidae) and *S. parsonsi* (Eurysternidae).

The lower jaw of *O. borsukbialynickae* differs from *S. parsonsi* in a much shorter triturating surface and presence of two well-developed and parallel lingual and labial ridges. In *S. parsonsi*, the labial and lingual ridges are lacking (Gaffney, 1975b; Joyce, 2000; Parsons & Williams, 1961). On the other hand, all the plesiochelyids with preserved mandibles (*Plesiochelys etalloni*, *P. planiceps*, and *P. mcdowelli*), with the exception of *Portlandemys gracilis* (Anquetin, Püntener, & Billon-Bruyat, 2015), from the Kimmeridgian of Switzerland, have a much more pronounced lingual ridge of the mandible, a relatively wide triturating surface and the symphyseal hook (Anquetin et al., 2015; Gaffney, 1976; Parsons & Williams, 1961). The expansion of the mandibular triturating surface in all three cases appears to be attained differently. In most plesiochelyids, the lingual ridges of the mandible moved medially, decreasing the distance and an angle between them and increasing the width of the trough separating them from the labial ridges. In *P. mcdowelli*, the anterior sections of the lingual ridges meet along the midline resulting in caudal elongation of the symphyseal area (Gaffney, 1975a, 1976; Parsons & Williams, 1961). Two more plesiochelyid taxa, *Craspedochelys jaccardi* (Pictet, 1860) from the Kimmeridgian and Early Tithonian of Switzerland and France and *Craspedochelys picteti* (Rütimeyer, 1873), from the Kimmeridgian of Switzerland are not represented by any cranial or comparable postcranial material. In *S. parsonsi*, the lingual ridge is much weaker, but the presence of the symphyseal median trough, the narrowness of the posterior border of the symphyseal area, and its closeness to the anterior coronoid border (Gaffney, 1975b; Joyce, 2000; Parsons & Williams, 1961) may be a relic of a similar process, possibly mirroring the modifications of the maxilla towards the acquisition of a secondary palate. Additional elongation of the symphysis, however, appears to have taken place rostrally, resulting in an exceptionally elongated snout of that turtle. In *O. borsukbialynickae*, however, the lingual ridges are widely separated and the posterior limit of the symphyseal area is wide, suggesting only the rostral expansion of the symphysis. No data is available concerning the morphology of the mandible of aff. *Solnhofia* spp. from Cerin, France (Broin, 1994), but no large differences are expected. The other Late Jurassic turtles with preserved mandible, *Portlandemys gracilis* and *Eurysternum wagleri* (Meyer, 1839), have shorter symphyses and, in the case of *E. wagleri*, a wider angle between the rami (figure 1 in Anquetin & Joyce, 2014; Anquetin et al., 2015). The lower jaws of *Jurassichelon oleronensis* (Pérez-García, 2015a), and *Palaeomedusa testa* (Meyer, 1860), are unknown, but the skulls of these taxa possess wide, rounded, and short snouts unable to accommodate an elongated and narrow mandibular symphysis (Joyce, 2003; Meyer, 1860; Rieppel, 1980). The Tithonian South American marine turtle *Neusticemys neuquina* (Fernandéz & de la Fuente, 1988) appears to have a similar outline of the symphysis (Gasparini, Spalletti, & de la Fuente, 1997) as *O. borsukbialynickae*, but this taxon is not known from Europe (although closely related to European *S. parsonsi* and *Jurassichelon oleronensis*—see de la Fuente, Sterli, & Fernandéz, 2014) and no data is available about the morphology of the oral surface of its mandible. The overall morphology of the mandible appears to be very similar to that of the Cretaceous basal protostegids *Chelospharghis advena* (Hay, 1908), *Calcarichelys gemma* (Zangerl, 1953), and *Bouliachelys suteri* (Kear & Lee, 2006), but the sagittal crest of *O. borsukbialynickae* is lower and blunter (see figure 21C in Zangerl, 1953, and figure 5 in Hooks, 1998). It also resembles the mandible of modern *Caretta caretta* (Linnaeus, 1758; Wyneken, 2001). This may suggest similar feeding ecology in these taxa but may also have a phylogenetic value. The Late Jurassic eurysternids and *Jurassichelon oleronensis* in some phylogenetic analyses were recovered in a clade with basal protostegids (Cadena & Parham, 2015; Joyce, 2007) and, in the case of de la Fuente et al. (2014), also with *Neusticemys neuquina*. On the other hand, the basalmost known protostegids have short mandibular symphyses (Cadena & Parham, 2015; Hirayama, 1998), so homoplasy cannot be ruled out.

The coracoid of *O. borsukbialynickae*, with rather thick and short neck and symmetrical, triangular plate, differentiates that animal from *Eurysternum wagleri*, *Parachelys eichstaettensis* (Meyer, 1864), *Plesiochelys etalloni*, *Thalassemys hugii* (Rütimeyer, 1873), and *Tholemys passmorei* (Andrews, 1921). *Eurysternum wagleri* had slightly asymmetrical coracoid plate and a long, constricted coracoid neck (figure 1 in Anquetin & Joyce, 2014); most probably erroneously, the coracoid foramen was reported in that turtle by Jaekel (1918). The coracoid of *Thalassemys hugii* is closest in morphology to the coracoid of *O. borsukbialynickae*, but its neck is proportionally narrower and longer (Bräm, 1965). The coracoid plate of *Tholemys passmorei* and *Plesiochelys etalloni* is noticeably wider and has a slightly different shape, with robust expansion of the proximal part in *Tholemys passmorei* and noticeable asymmetry of *Plesiochelys* coracoid plate (Andrews, 1921; Bräm, 1965). *Parachelys eichstaettensis*, on the other hand, had a narrow, elongate coracoid plate (Meyer, 1864).

The femur of *O. borsukbialynickae* also seems to differ from *S. parsonsi* femur. *O. borsukbialynickae* femur has a U-shaped intertrochanteric fossa. *S. parsonsi* femur is said to have a V-shaped intertrochanteric fossa (Joyce, 2000). Such a difference may have some locomotory implications, but the trochanters of *O. borsukbialynickae* are broken and a lack of adequate illustrations of *S. parsonsi* makes the comparisons difficult. Other differences in the proximal head of the femur exist between *O. borsukbialynickae* and *Tropidemys langii* (Rütimeyer, 1873). The femoral head of the latter is weaker developed than in *O. borsukbialynickae*, and the trochanters seem to be directed more rostrocaudally, leaving wider, more circular intertrochanteric fossa (Püntener, Billon-Bruyat, Bocat, Berger, & Joyce, 2014). No material comparable with *O. borsukbialynickae* is known for *Tropidemys seebachi* (Portis, 1878), from the Kimmeridgian of Hannover and *Tropidemys* (*Pelobatochelys*) *blakii* (Seeley, 1875) from the Tithonian of England, but no great variation is expected. The distal articular surfaces of the *O. borsukbialynickae* femur are prominent and well developed, even though the type specimen is subadult. That is the next difference between *O. borsukbialynickae* and most other Late Jurassic turtles, including *S. parsonsi* and *Palaeomedusa testa*, that have weakly developed articular structures (Joyce, 2000, 2003). Particularly in *I. fitzingeri* (Meyer, 1839b), and *Enaliochelys chelonia* (Seeley, 1869), the morphology of the femur is notably different, mainly due to much weaker development of proximal and distal articular structures in these taxa (Pérez-García, 2015a; Rütimeyer, 1873). The angle at which the femoral head is turned relative to the shaft in *O. borsukbialynickae* is apparently lower than in *Enaliochelys chelonia* (see Pérez-García, 2015a).

Thalassemys hugii appears to differ from *O. borsukbialynickae* in the morphology of the ilium. In *O. borsukbialynickae*, the ventral, acetabular portion of the ilium is expanded, the ilial neck is constricted, and the dorsal fan is well developed and elongated posteriorly. The ventral end of the ilium is less expanded, and the ilial neck more uniform in *Thalassemys hugii* figured by Bräm (1965) and an indeterminate thalassemydid figured by Wellnhofer (1967). *Thalassemys hugii* also seems to have a noticeable anterior expansion of the dorsal fan (Bräm, 1965). The elongated dorsal fan on the drawing by Bräm may be exaggerated, taking into account the photograph of the specimen (plate 7 in Bräm, 1965) and Wellnhofer's pictures. On the other hand, *Thalassemys bruntrutana* (Püntener, Anquetin, & Billon-Bruyat, 2015), specimen from England, figured and described by Pérez-García (2015b), has notably different morphology of the ilium—much shorter and more robust with more expanded ventral section and posterior process longer than in *O. borsukbialynickae*. This dissimilarity may be attributed to interspecific differences, but the high degree of compaction (Püntener et al., 2015) and apparent slight differences in the shape of both preserved ilia (figure 3C,D,Q in Pérez-García, 2015a) suggest that it may be partially caused by deformation and crushing. Currently, no comparable material is known for *Thalassemys marina* (Fraas, 1903), from the Tithonian of Schnaitheim. The ilium of *Craspedochelys jaccardi*, schematically figured by Bräm (1965), also has a less expanded ventral part, but the posterior process of the dorsal fan is clearly more elongated and, differently than in *O. borsukbialynickae*, bent ventrally. The ilium of *Anaphotidemys wittei* (Maack, 1869), as figured in the original description, appears to have a similar extent of ventral expansion, but its neck seems to be wider and the posterior process of the dorsal fan is much smaller and differently shaped. Unlike the coracoid and mandible, the ilium of *O. borsukbialynickae* is nearly identical to that of *Eurysternum wagleri* (figure 2 in Anquetin & Joyce, 2014).

Several taxa also differ from the new Polish specimen in size. Both *S. parsonsi* as well as *I. fitzingeri* were amongst the smallest Jurassic turtles, the length of *S. parsonsi* carapace oscillated around 20 cm, and *I. fitzingeri* was even smaller, while *Thalassemys hugii* reached around 60 cm and more in carapace length (Joyce, 2000; Pérez-García, 2015a). The estimated length of *O. borsukbialynickae* carapace (based on its femur length) is 50 cm and the holotype is most likely not fully grown.

Currently, there exists no comparable material that would support or refute the synonymy of *O. borsukbialynickae* with poorly preserved *Hydropelta meyeri* (Thiollière, 1850), from the Kimmeridgian of France, and *Euryaspis radians* (Wagner, 1861), from Solnhofen. These two taxa, however, are based on fragmentary specimens lacking truly diagnostic characters and exhibit some features that may suggest their synonymy with *Eurysternum wagleri* or *Solnhofia* sp. (Anquetin & Joyce, 2014; Broin, 1994; Lapparent de Broin, 2001).

The gathered material of *O. borsukbialynickae*, while apparently specifically diagnostic, is not sufficient to perform a phylogenetic analysis or to determine its affiliation to any suprageneric taxa. This stresses the need to elaborate on all the available skeletal elements of Jurassic turtles in future studies. While there exist numerous nearly complete Jurassic eucryptodiran specimens from different localities in Europe (e.g., Anquetin & Joyce, 2014; Bräm, 1965; Joyce, 2003), most of the attention is usually devoted only to the cranium and shell, while the girdles and appendicular skeleton are often described very briefly and pictured inadequately, if at all. While it is true that these elements are closely linked to the life environment, thus prone to homoplasy and therefore of limited use for global phylogenetic analyses, they may be very useful for phylogenies or comparisons on a smaller scale. For example, our survey of the literature indicates that there are notable differences in the morphology of ilium and coracoid in various eucryptodiran taxa (see above). Nonetheless, it is difficult to evaluate the distribution and range of variability of these observed morphologies, because the adequate illustrations allowing comparisons are very rare and paradoxically largely restricted to the works from the 19th century. It is especially surprising nowadays, when modern imaging techniques, like computed tomography or X-ray, are affordable and allow insight into previously unavailable details of morphology without even resorting to the troubles of fossil preparation.

7 | PALAEOECOLOGY

The palaeoecology of the Late Jurassic turtles has been intensively debated in the past. Modern turtle species exhibit a full spectrum of ecologies, from fully terrestrial, through varied degrees of semi-aquatic, to fully pelagic (e.g., Joyce & Gauthier, 2004). Unfortunately, the interpretation of the ecology of fossil turtles is usually difficult. The most reliable methods that allow assessing the habitat preferences of these animals consist of histological sampling of the shell (Scheyer & Sander, 2007) or the measurement of the forelimb proportions (Joyce & Gauthier, 2004). These methods are unusable for fragmentary and very scarce bones (which are obviously inadequate for destructive analysis), and even for more complete and common taxa, it is usually impossible to distinguish between freshwater and coastal marine ecologies. Therefore, commonly, a much less reliable approach is used, and the habitat preference is assumed based on the shell morphology (if preserved) and the sedimentary environment in which the fossils were found.

It is currently accepted that during the Middle Jurassic, turtles returned to an aquatic setting after a period of inhabiting terrestrial environments lasting since the Norian (Anquetin, 2011; Joyce & Gauthier, 2004; Scheyer & Sander, 2007). The histology and morphology as well as the sedimentary environments indicate that *Eileanchelys waldmani* (Anquetin, Barrett, Jones, Moore-Fay, & Evans, 2009), from the Middle Jurassic Kilmaluag Formation in Scotland, *Heckerocherlys romani* Sukhanov, 2006, from the Middle Jurassic of Peski locality, Moscow Region, Russia, and *Condorchelys antiqua* (Sterli, 2008), from the Middle to Upper Jurassic limestones and mudstones of Cañadon Asfalto Formation in Argentina were probably the earliest Jurassic aquatic turtles (Cerda, Sterli, & Scheyer, 2016; Scheyer, 2014). Similarly, the Late Jurassic turtles from the lithographic limestones of Solnhofen in southern Germany and other European localities, classically assigned to four families (*Pancryptodira*: Eurysternidae, Plesiochelyidae, and Thalassemydidae; *Pleurodira*: Platychelyidae), show many aquatic adaptations. Traditionally, they are considered to be marine; however, the oxygen isotope compositions of the turtle bones from the Chassiron, Crayssac, Canjuers, Cerin, and Solnhofen regions clearly indicate both marine (Plesiochelyidae and *Jurassichelon oleronensis*, although its affinities are controversial—see Pérez-García, 2015a) and freshwater or brackish (specimens referred to "Thalassemydidae" by Billon-Bruyat, Lécuyer, Martineau, & Mazin, 2005, but in fact including mostly or solely the eurysternid turtles) life environments (Billon-Bruyat et al., 2005). This is further supported by the large interorbital foramina present in plesiochelyids, indicating the presence of large salt glands in these animals—an adaptation necessary to cope with the increased water salinity (e.g., Billon-Bruyat et al., 2005). According to these data, only plesiochelyids and *Jurassichelon oleronensis* should be considered to be true European coastal turtles. Eurysternids and possibly thalassemydids likely remained in fresh or brackish water, only rarely, if at all, reaching fully saline coastal waters and being at most intermediate between the fully terrestrial or freshwater turtles and marine forms. Still, given the spotty sampling, it is possible that other taxa belonging to these families represented other ecologies. On top of that, despite the recent progress, the definitions and content of the three pancryptodiran families from Solnhofen, Solothurn, and other European localities is still rather confused, and they may in fact belong to one heterogeneous group (e.g., Anquetin, Deschamps, et al., 2014a; Anquetin, Püntener, et al., 2014b). It must be also noted that Billon-Bruyat et al. (2005) did not provide the numbers of specimens sampled nor enough data to verify whether the specimens used by them were correctly identified or how diagnostic they are, so there is some uncertainty about the obtained results and possibly this interpretation may change in the future.

Dietary specializations of the Solnhofen turtles are poorly known. Some of them were possibly durophagous. Some specimens of the pancryptodiran turtle *Eurysternum wagleri* were found with echinoderms in their stomach region. That was proposed as an argument for marine ecology of this turtle (Joyce, 2015), but such a life environment seems to be incongruent with the isotope compositions, indicating that at least most of the food of these animals was supplied by fresh or semi-saline waters (Billon-Bruyat et al., 2005; however, see the notion above). The pancryptodiran turtle *S. parsonsi* has a huge skull with extended snout and well-developed secondary palate (Gaffney, 1975b; Joyce, 2000; Parsons & Williams, 1961). These were probably adaptations to a durophagous life style that facilitated crushing of hard-shelled animals, similarly to expanded triturating surfaces and secondary palate in modern and fossil marine turtles (Parham & Pyenson, 2010). *O. borsukbialynickae* has a massive lower jaw. The snout is short in comparison with *S. parsonsi* (possibly optimizing the bite force), but the spoon-like symphysis is thick and forms a solid crushing surface. The wide triturating surface is a clear adaptation to durophagy, and as such, it would imply an aquatic, or at least semi-aquatic, mode of life for *O. borsukbialynickae*, suggesting that it fed mostly on hard prey. On the other hand, elevated labial ridge seems to be not designed for crushing the hardest and largest molluscs. *O. borsukbialynickae* might have used the spoon-like snout to pick up selected hard-shelled invertebrates, like smaller bivalves and decapod crustaceans, from the seafloor and subsequently crush them with its wide triturating surface (Figure 5). just like that of the modern loggerheads (*Caretta caretta*), possessing a similarly built mandible (Parham & Pyenson, 2010). The bivalves and decapods are frequent invertebrates in Owadów-Brzezinki Quarry (Feldmann et al., 2015; Kin et al., 2013), so they were probably in the range of *Owadowia* diet. The mandibular rami of *O. borsukbialynickae* meet at an angle of about 35°. This is comparable to the value found in extant sea turtles, where the range is from 35° to 50° (Carr, 1952; Zangerl, Hendrickson, & Hendrickson, 1988). Some members of the Cretaceous Protostegidae family are also characterized by lower values (i.e., 25° in *Archelon ischyros* Wieland, 1869; see Nicholls, Tokaryk, & Hills, 1990). The noticeably longer snout of *S.parsonsi*, resembling that of modern *Eretmochelys imbricata* (Linnaeus, 1766; Gaffney, 1975b; Joyce, 2000; Wyneken, 2001), may suggest similar diet, consisting of marine sponges (Parham & Pyenson, 2010), but currently, there is no data that would unambiguously support a marine ecology of that eurysternid.

FIGURE 5 *Owadowia borsukbialynickae*, life restoration during feeding on decapod crustacean. Digital painting by T. Szczygielski [Colour figure can be viewed at wileyonlinelibrary.com]

There is no data on the morphology of the forelimb of *O. borsukbialynickae* nor any shell material is known that could be used for histological analysis, but an aquatic habitat for *O. borsukbialynickae* is strongly suggested by the morphology of its mandible and the exceptionally good state of bone preservation, indicating no extended exposure to weathering, little to no post-mortem transport, and quick burial. Although the specimen is fragmentary, the presence of associated mandible, femur, and girdle bones without any shell elements may be explained by the patterns of decay observed for *Trachemys scripta* in the aquatic environment (Brand, Hussey, & Taylor, 2003). During the "bloat and float" phase of decay the disarticulation proceeds gradually, and the skull, limb, and girdle bones are generally early to disarticulate (within under 4 months at room temperature, supposedly faster in hotter climate), while the rest of the body is still floating (Brand et al., 2003). A possible taphonomic scenario, therefore, may be proposed: The specimen died in the water or a fresh cadaver was transported from the shore soon after death. Then, the dermis began to lose its integrity and the floating body started to disarticulate. Small, light bones (distal limb bones, vertebrae) might have been transported by the currents or lost somewhere else due to prior drifting of the corpse, while the larger and heavier ones (femur, girdle elements, massive mandible) sank quickly and were buried together. The shell and possible remaining skeletal parts then drifted away and eventually settled elsewhere.

It is currently impossible to decide whether *O. borsukbialynickae* preferred freshwater or saline waters. Kin et al. (2013) described the Owadów-Brzezinki locality as a lagoon or shallow marine basin, similar to the Solnhofen lithographic limestone basins. It is possible, however, that the turtle-yielding horizon of Owadów-Brzezinki was more distant from the coast than Solnhofen lagoons, as evidenced by the lack of freshwater and brackish animals.

8 | CONCLUSIONS

A new pancryptodiran turtle, *O. borsukbialynickae*, is described from the Tithonian lagoon limestones of Owadów-Brzezinki Quarry, Poland. The most characteristic trait of this new taxon is its expanded triturating surface indicating a durophagous ecology. The morphology of *O. borsukbialynickae* mandible is unlike that any other Jurassic turtle known thus far, but rather resembles the Cretaceous protostegids and recent cheloniids, which suggests that this turtle might have inhabited a similar trophic niche. While it is possible that *O. borsukbialynickae* was a semiaquatic or freshwater turtle, the lower jaw morphology and its inferred feeding preferences make such assumption unlikely, and rather suggest that this animal spent a lot of time in a shallow water, possibly marine environment, like Owadów-Brzezinki lagoons. The taphonomic evidence (the quantitative dominance of marine vertebrates in the Owadów-Brzezinki bone-bed, lack of any brackish and freshwater taxa, and absence of transportation) suggests that *O. borsukbialynickae* was an inhabitant of these lagoons, rather than a terrestrial animal that inhabited the adjacent land. Such assumptions may be supported in the future by new finds and isotope data.

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