A new genus and tribe of freshwater mussel (Unionidae) from Southeast Asia

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The freshwater mussel genus *Oxynaia* Haas, 1911 is thought to be comprised of two geographically disjunct and morphologically variable species groups but the monophyly of this taxon has yet to be tested in any modern cladistic sense. This generic hypothesis has important systematic and biogeographic implications as *Oxynaia* is the type genus of the currently recognized tribe Oxynaiini (Parreysiinae) and is one of the few genera thought to cross several biogeographically important barriers in Southeast Asia. Morphological and molecular data clearly demonstrate that *Oxynaia* is not monophyletic, and the type species and its allies (*O. jourdyi* group) belong to the Unioninae, and more specifically as members of the genus *Nodularia* Conrad, 1853. Therefore, neither *Oxynaia* syn. nov. nor Oxynaiini Starobogatov, 1970 are applicable to the Parreysiinae and in the absence of an available name, *Indochinella* gen. nov. and Indochinellini trib. nov. are described. Several combinations are proposed as follows: *Indochinella pugio* (Benson, 1862) gen. et comb. nov., *Nodularia jourdyi* (Morlet, 1886) comb. res., *N. gladiator* (Ancey, 1881) comb. res., *N. diespiter* (Mabille, 1887) comb. res. and *N. micheloti* (Morlet, 1886) comb. res. Finally, we provide an updated freshwater biogeographic division of Southeast Asia.

Integrative taxonomic studies are of substantial practical importance to conservation stakeholders as accurate information on the systematics and distributions of biodiversity forms the foundation of taxon- and habitat-based conservation efforts. The application of basic systematic and phylogenetic research has played a critical role in the conservation of freshwater mussels (Bivalvia: Unionidae), which are among the most threatened groups of animals worldwide. However, the vast majority of recent systematic research has focused on the North American and European fauna, while the comparatively diverse tropical lineages have received disproportionately less attention. Although, several recent systematic efforts focused on Asian lineages have dramatically improved our understanding of the classification, morphological evolution, and biogeography of many tropical freshwater mussel clades, many biographically interesting and systematically important taxa remain poorly understood from a phylogenetic perspective. This is particularly true of the genus *Oxynaia*, which has an unusual disjunct geographic distribution in Myanmar and northern Vietnam and is the type genus of the tribe Oxynaiini Starobogatov, 1970.

Whelan et al.\(^10\) recently transferred the tribe Oxynaiini from the subfamily Amblemiinae to the Parreysiinae on the basis of recovering *Oxynaia pugio* (Benson, 1862) among the latter subfamily in a molecular phylogeny. Whereas, traditional morphological classifications consistently consider *Oxynaia* a member of the subfamily Unioninae (in its various usages\(^1\text{–}^4\)). However, these seemingly irreconcilable subfamily-level classifications of *Oxynaia* (Unioninae vs Parreysiinae) have relied primarily on only one of the two geographically disjunct species groups, suggesting that *Oxynaia* may not be monophyletic.

Species in the genus *Oxynaia* each share the presence of a strongly pointed posterior end (Greek: oxy – ‘sharp’), but can be divided into two distinct geographic species groups, the *O. jourdyi* group and the *O. pugio* group\(^15\) (Fig. 1). The *Oxynaia jourdyi* group includes four putative species from northern Vietnam: *O. jourdyi*...
(Morlet, 1886) (generic type), *O. gladiator* (Ancey, 1881), *O. despiter* (Mabille, 1887), and *O. micheloti* (Morlet, 1886). The *Oxynaia pugio* group contains a single described species (*O. pugio*) from Myanmar.7,10,14

Our objective herein is to test the monophyly of the genus *Oxynaia*, evaluate the morphological traits of the resultant suprageneric clades containing *Oxynaia* species, and to make the appropriate taxonomic changes to more accurately reflect our hypotheses of evolutionary history.

**Results**

**Phylogenetic analyses.** Our family-level phylogenetic analyses based on mitochondrial and nuclear markers (five partitions: three codons of COI + 16S rRNA + 28S rRNA) reveals that *Oxynaia* is not monophyletic (Fig. 2). *Oxynaia jourdyi* is well supported as a member of the subfamily Unioninae, whereas *O. pugio* is recovered in the distantly related subfamily Parreysiinae. *Oxynaia jourdyi* is resolved in a shallow and strongly supported clade comprised of representatives of the genus *Nodularia* Conrad, 1853 (BS/BPP = 100). The *Oxynaia pugio* is recovered in a well-supported clade with the genus *Radiatula* Simpson, 1900. The genus *Indonaia* Prashad, 1918

![Map of distribution ranges of the two *Oxynaia* species groups in Southeast Asia](https://www.nature.com/scientificreports/)

**Figure 1.** Map of distribution ranges of the two *Oxynaia* species groups in Southeast Asia (see Taxonomic Account for details). The map was created using ESRI ArcGIS 10 software (www.esri.com/arcgis); the topographic base of the map was created with Natural Earth Free Vector and Raster Map Data (www.naturalearthdata.com). (Map: Mikhail Yu. Gofarov).
appears to be the closest relative of the Oxynaia pugio + Radiatula clade, but with only moderate support values (BS = 61; BPP = 81).

**Morphological analyses.** Comparisons of the soft anatomy and larval morphology of representatives of the major freshwater mussel clades in the Oriental Region clearly demonstrate the polyphyly of Oxynaia s. lato (Table 1). The Oxynaia jourdyi group is unambiguously placed in the subfamily Unioninae by the combination of ectobranchous brooding condition and hooked larvae with basal spines, known synapomorphies of the Unioninae. The Oxynaia pugio group (=Indochinella gen. nov.) is united with all other members of the subfamily Parreysiinae on the basis of possessing a tetragenous brooding condition (sans Lamellidentini Modell, 1942 = ectobranchous), unhooked glochidia, as well as having the ascending lamella of the inner demibranchs attached to the visceral mass across their entire length (vs. attached only anteriorly in the Unioninae). This combination of traits is a novel method of recognizing the Parreysiinae (sans Lamellidentini). Several shell characters also unite the Oxynaia jourdyi group with representatives of the Unioninae, especially Nodularia, including the position, elevation, and sculpturing of the umbo, as well as several features of the dentition (Table 2 and Fig. 3). Nodularia differs from Indochinella gen. nov. by having a very pronounced and elevated umbo (vs. not pronounced and not elevated), umbo location in the first half of the shell (vs. in the first third), nodulose wrinkle umbo sculpture (vs. v-shaped), and a rectangular and sharp anterior pseudocardinal tooth and a thick and pyramidal posterior pseudocardinal tooth in the left valve (vs. two separated ribbed teeth placed in parallel line with one another).

The combination of the molecular phylogeny, soft anatomy, larval characters, and shell morphology clearly demonstrate the polyphyly of Oxynaia s. lato. The type species and its allies (i.e. the Oxynaia jourdyi group) are unambiguously placed in the subfamily Unioninae, rendering both Oxynaia and Oxynaiini inapplicable to the Parreysiinae. The tribe Oxynaiini Starobogatov, 1970 is herein recognized as an available family-group level name of the Unioninae Rafinesque, 1820. In the absence of an available name for the Oxynaia pugio species group and the larger Parreysiinae clade including the O. pugio group, Radiatula, and Indonedia (i.e. the former Oxynaiini), the genus Indochinella gen. nov and tribe Indochinellini trib. nov. are described here.

**Range disjunction.** The two species groups of Oxynaia have clearly distinct ranges (Fig. 1). All the reliable records (mostly type localities, see Taxonomic Account) of the Oxynaia jourdyi species group are concentrated within the Red, Cà and Câu River drainage basins of northern Vietnam. The Oxynaia pugio species group is known from the Irrawaddy, Sittaung and Tavoy River drainages. Neither species group occurs in the drainages situated between eastern Myanmar and northern Vietnam (i.e., Salween, Mae Klong, Chao Phraya, and Mekong). Zieritz et al. listed two species, Oxynaia gladiator and O. micheloti, from the Mekong River but those reports refer to misidentified specimens (MNHN IM-2014-6880) or suspect localities (FMNH 20402 and NCSM 84425).
Taxonomic Account

Family Unionidae Rafinesque, 1820
Subfamily Unioninae Rafinesque, 1820

Type genus: *Unio* Philipsson in Retzius, 1788

Genus *Nodularia* Conrad, 1853
Type species: *Unio douglasiae* Griffith & Pidgeon, 1833 (by original designation)
Type locality: Unknown.

Comments: We recognize *Oxynaia* as a junior synonym of *Nodularia*, and transfer the four Vietnamese species previously treated as *Oxynaia* to *Nodularia* as well. Additionally, we considered *Nodularia dorri* as the fifth member of this group. The close geographic proximity of the type localities and the conchological similarity of the named taxa raises questions about their validity and deserves further research.

*Nodularia douglasiae* (Griffith & Pidgeon, 1833) comb. res.

Unio douglasiae Griffith (1881): p. 468; *Nodularia douglasiae* Simpson (1914): p. 99; Haas (1913): p. 152.

Type locality: Tonkin. Environs de Dang-son (Đặng Sơn) [p. 77]; Bac-Hat (Bắc Hà), étangs du bord de la rivière Claire (Jourdy) [p. 290].

Distribution: Red and Cả River drainage basins, northern Vietnam.

*Nodularia gladiator* (Ancey, 1881) comb. res.

Unio gladiator Ancey (1881): p. 468; *Nodularia gladiator* Simpson (1914): p. 99.

Type locality: Yon-Bag, Tonkin.

Distribution: Red River drainage basin, northern Vietnam. Record from the Mekong Basin is erroneous.

*Nodularia diespiter* (Mabille, 1887) comb. res.

| Taxon                        | Voucher no. | Inner demibranch ascending lamella fusion to visceral mass | Brooding     | Glochidia | Higher classification |
|-----------------------------|-------------|-----------------------------------------------------------|--------------|-----------|-----------------------|
| Lamellidens marginalis (Lamarck, 1819) | CAS180833   | Complete                                                   | Ectobranchous| Unhooked  | Parreysiinae: Lamellidintini |
| Parreysia corrugata (Müller, 1774) | N/A9,10     | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Parreysiini |
| Leoparreysia burmana (Blanford, 1869) | CAS180831   | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Leoparreysiini |
| Coelatura sp.               | UF 510905   | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Coelaturini |
| Indonaia caerulea (Lea, 1831) | UF507572    | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Indochinellini |
| Radilula aff. humilis sp.2  | UF 507848   | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Indochinellini |
| Indochinella pugia (Benson, 1862) gen. et comb. nov. | CAS180796, CAS189963 | Complete                                                   | Tetragenous  | Unhooked  | Parreysiinae: Indochinellini |
| Nodularia douglasiae (Griffith & Pidgeon, 1833) | RMBH: biv227_12, biv132, biv134 | Anterior end                                             | Ectobranchous| Triangular, hooked | Unioniniae |
| Oxynaia micheloti (Morlet, 1886) * | NCSM 84920, NCSM 84425 | Anterior end                                             | Ectobranchous| Triangular, hooked | Unioniniae |
| Pyganodon granulis (Say, 1829) | UF369750    | Anterior end                                             | Ectobranchous| Triangular, hooked | Unioniniae |
| Rectidens sumatrensis (Dunker, 1852) | UF410001   | Anterior end                                             | Ectobranchous| n/a       | Rectidentiniae: Rectidentini |
| Contraakens contradens (Lea, 1838) | UF507874, UF507591 | Anterior end                                             | Ectobranchous| n/a       | Rectidentiniae: Contradentini |
| Monodonta vombruchiana (Lea, 1840) | UF507565, UF507438 | Anterior end                                             | n/a          | n/a       | Pseudodontiniae: Pilsbryoconchini |
| Pilsbryoconcha sp. | UF507453   | Anterior end                                             | Tetragenous  | Unhooked  | Pseudodontiniae: Pilsbryoconchini |
| Chamberlainia hainesiana (Lea, 1856) | UF507722, UF507872 | Complete                                                   | n/a          | n/a       | Gonideiniae: Chamberlainini |

Table 1. List of conchological and anatomical characters in Parreysiinae and other selected subfamilies of the Unionidae. n/a – not available. *We used this species as a representative of the *Oxynaia jourdyi* group, because gravid individuals of the type species of this genus were not available.
Table 2. Comparative analysis of the genera *Indochinella* Bolotov, Pfeiffer, Vikhrev & Konopleva gen. nov., *Oxynaia* Haas, 1911, and *Nodularia* Conrad, 1853 on the basis of conchological features. *Based on the two syntypes (MNHN-IM-2000-33685, Coll. du Journal de Conchyliologie, ex Coll. Morlet; type locality: Tonkin. Environ de Dang-son (Jourdy) [p. 77]18; Bac-Hat, étangs du bord de la rivière Claire (Jourdy) [p. 290]18. **Based on a sample from Soldatskoe Lake, Razdolnaya River Basin, Russian Far East (RMBH no. biv_227_12)

| Conchological features | *Unio pugio* Benson, 1862, the type species of the genus *Indochinella* | *Unio jourdyi* Morlet, 1886, the type species of the genus *Oxynaia* | *Unio douglassiae* Griffith & Pidgeon, 1833, the type species of the genus *Nodularia* |
|------------------------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|
| Shell shape            | Cuneiform                                       | Somewhat cuneiform, with more height, anteriorly rounded, posteriorly elongated and pointed | Oval-form, slightly narrow in the posterior part |
| Umbo                   | Not pronounced                                  | Very pronounced, elevated                       | Very pronounced, elevated                        |
| Umbo sculpture         | V-shaped                                        | Nodulose wrinkles                              | Nodulose wrinkles                               |
| Umbo position          | In the first third of the shell                 | In the first half of the shell                 | In the first half of the shell                  |
| Pseudocardinal teeth   | Two separated ribbed teeth placed in parallel line with one another | Anterior tooth rectangular and sharp, posterior tooth thick and pyramidal | Anterior rectangular, sharp and ribbed, posterior tooth small and pyramidal |
| of the left valve       |                                                 |                                                 |                                                 |
| Pseudocardinal teeth   | Anterior tooth reduced, posterior tooth somewhat pyramidal and wrinkled | Anterior tooth lamella-shaped, posterior tooth rectangular, wrinkled | Anterior tooth reduced, lamella-shaped, posterior tooth somewhat trapeziform and ribbed |
| of the right valve      |                                                 |                                                 |                                                 |
| Lateral teeth          | Rather short, two teeth on the left and one tooth on the right valve | Long, two teeth on the left and one tooth on the right valve | Straight, elongate, sharp with small scratches, two teeth on the left and one tooth on the right valve |

*Unio diespiter* Mabille (1887): p. 162; Simpson (1900): p. 861.  
*Nodularia diespiter* Simpson (1914): p. 993.  
*Oxynaia diespiter* Haas (1911): Pl. 15; Haas (1913): p. 154.

**Type locality:** Tonkin.

**Distribution:** Red River drainage basin, northern Vietnam.

*Nodularia micheloti* (Morlet, 1886) comb. res.  
*Unio micheloti* Morlet (1886): p. 77.  
*Nodularia micheloti* Simpson (1900): p. 814.  
*Oxynaia micheloti* Haas (1911): Pl. 14; Haas (1913): p. 156.

**Type locality:** Tonkin, environs de Chu.

**Distribution:** Cầu River drainage basin, northern Vietnam. Record from the Mekong Basin is erroneous.

*Nodularia dorri* (Wattebled, 1886)  
*Unio dorri* Wattebled (1886): p. 71.  
*Nodularia dorri* Simpson (1900): p. 809.  
**Type locality:** Les arroyos des environs de Huet.

**Distribution:** Perfume River, central Vietnam. Zieritz *et al.* erroneously listed *N. dorri* as an endemic species of the Mekong Basin.

**Subfamily Parreysiinae Henderson, 1935**  
**Type genus:** *Parreysia* Conrad, 1853

**Comments:** This subfamily includes five tribes: Parreysiini Henderson, 1935, Coelaturini Modell, 1942, Lamellidentini Modell, 1942, Leoparreysiini Vikhrev, Bolotov & Kondakov, 2017 and Indochinellini trib. nov., a new tribe described here.

**Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva trib. nov.**  
**Type genus:** *Indochinella* Bolotov, Pfeiffer, Vikhrev & Konopleva gen. nov.

**Figures 3a and 4**

**Diagnosis:** The Parreysiini and Leoparreysiini are the most morphologically similar family-group level taxa to the Indochinellini. However, the Indochinellini can be distinguished from the Parreysiini and Leoparreysiini by having a much more elongate shell outline (vs. circular) and a nearly straight to convex ventral margin (vs. strongly convex).

**Description:** Adults small (22 mm) to medium (54 mm) sized for family. Shell outline narrow, elongate, strongly inequilateral, always with a straight or convex ventral margin. Moderately inflated, posterior ridge rounded with moderately to very steep posterior slope. Umbo only slightly elevated above hinge line usually with v-shaped umbo sculpture. Green zigzag sculpturing on shell disc common, but absent in some individuals and taxa, e.g., *Indonaisa caerules* (Lea, 1831), *Radiatula humilis* (Lea, 1856), *R. pilata* (Lea, 1866), and *Indochinella pugio* gen. et comb. nov. Shells moderately thick. Pseudocardinals erect and stumpy to long and bladelike; two in left valve (may become one in blade-like teeth) and one in right valve occasionally with a second rudimentary anterior tooth. Laterals are moderately short and diverging; two in left, one in right. Unhooked glochidia brooded in all four gills. Mantle margin ventral to incumbent aperture with many prominent blade-like papillae. Incurrent aperture papilose, excurrent and supra-anal apertures smooth. Ascending lamella of inner demibranch attached to visceral mass for its entire length.
Distribution: Southeast and South Asia.

Comments: This tribe includes at least three valid genera: *Indochinella* gen. nov., *Radiatula* Simpson, 1900, and *Indonaia* Prashad, 1918.

**Genus Indochinella** Bolotov, Pfeiffer, Vikhrev & Konopleva gen. nov.

Type species: *Unio pugio* Benson, 1862.

Type locality: Regione Ava [Mandalay].

Figure 3a, Tables 1 and 2

Etymology: The name of this genus is derived from the greater Indochinese Peninsula.

Diagnosis: The genus is distinguished from *Nodularia* by the presence of tetragenous brooding of unhooked glochidia (vs. ectobranchous brooding of hooked glochidia), as well as complete fusion of the ascending lamella of the inner demibranch to the visceral mass (vs. only anterior fusion) (Table 1). *Indochinella* gen. nov. can also be distinguished from *Nodularia* by the umbo being only slightly elevated above the hinge line (vs. strongly elevated), fine v-shaped beak sculpture (vs. wrinkled and nodular), triangular posterior pseudocardinal (vs. trapezoidal or rectangular), and moderately short lateral teeth (vs. elongate) (Table 2 and Fig. 3). Adult *Indochinella* (with exception of a lineage from the Tavoy River) can be distinguished from all other representatives of the tribe by the presence of a sharp posterior ridge (vs. rounded) and very steep posterior slope (vs. gradual). Pseudocardinal teeth in *Indochinella* also tend to be more strongly developed than in other Indochinellini.

Description: Shell moderately thick; elongate with rounded anterior end and strongly pointed posterior end. Posterior ridge sharp. Posterior slope steep. Umbo hardly elevated above hinge line, fine v-shaped umbo sculpture, shell disc smooth to strongly sculptured. Moderately inflated. Pseudocardinal teeth strong, two in the left
valve, one in the right. Laterals moderately short, two in left valve, one in right. Tetragenous brooding condition (occasionally ectobranchous), unhooked glochidia.

Distribution: The genus is primarily known from Myanmar in the Irrawaddy, Sittaung, and Tavoy River drainages. The genus may also inhabit several other river basins in Myanmar, e.g., the Great Tenasserim, Salween, and some coastal rivers of the Bay of Bengal. A few records from India (e.g., Assam) are in need of future studies because these specimens could have been collected within the Irrawaddy Basin.

Comments: We assigned a single described species to the genus, although the divergent molecular lineages from the Sittaung and Tavoy River drainage basins may be worthy of formal taxonomic recognition.

Indochinella pugio (Benson, 1862) gen. et comb. nov.

Unio pugio Benson (1862): p. 193.
Nodularia pugio Simpson (1900): p. 814.
Oxynaia pugio Haas (1911): Pl. 14; Haas (1913): p. 158.

Material examined: Myanmar: Irrawaddy River basin, Nant Phar Lake, 24.2972°N, 97.2610°E, 29.xi.2016, 4 specimens (RMBH nos. biv_258_1, biv_258_2, biv_258_4, and biv_258_5), Vikhrev leg. Myanmar: Irrawaddy River basin, Myaung Lake, 24.2387°N, 97.1658°E, 01.xii.2016, 4 specimens (RMBH nos. biv 268, biv 268_1, biv 268_2, biv 268_4, and biv 268_5), Vikhrev leg.
biv_268_2, and biv_268_4), Vikhrev leg. Myanmar: Irrawaddy River basin, Pauk In Lake, 21.81347°N, 95.19746°E, 13.x.2009, 5 specimens (CAS 180788), Pitotrowski et al. leg. Myanmar: Irrawaddy River basin, Irrawaddy River near Myingyan, 21.48187°N, 95.30501°E, 15.x.2009, 5 specimens (CAS 189963), Pitotrowski et al. leg., Myanmar: Irrawaddy River basin, Chindwin River near confluence with Irrawaddy, 21.498445°N, 95.26631°E, 09.x.2009, 5 specimens (CAS 180796), Pitotrowski et al. leg. Myanmar: Sittang River basin, Myit Kyi Pauk Stream, 18.9613°N, 96.4455°E, 26.xl.2016, 3 specimens (RMBH nos. biv_251_3, biv_251_1, and biv_251_2), Vikhrev leg. Myanmar: Tavoy River, 14.5012°N, 98.1557°E, 26.iv.2015, 26.iv.2015, 38 specimens (RMBH nos. biv_147_10, biv_147_3, biv_147_18, biv_148_4, biv_148_7, and biv_148_15 are sequenced), Bolotov leg.

Redescription: Shell shape cuneiform, elongated, inequilateral, not inflated, rather thick. Posterior ridge sharp, posterior slope steep. Maximum shell length 53.4 mm, height to 24.3 mm, width to 18.7 mm. Fine v-shaped sculpture on umbo, umbo only slightly elevated above hinge line. Periostracum smooth, grey-brown to yellow-green, with dark parts along the radial lines; nacre whitish. Left valve with two parallel rather short lateral teeth and two ribbed parallel pseudocardinal teeth. Right valve with a single slightly curved lateral tooth and two pseudocardinal teeth, anterior tooth reduced, posterior tooth high, ribbed and strong. Umbo cavity not very deep, nacre in umbo cavity commonly tinted peach to golden-brown. Anterior adductor scar well pronounced, funneled; posterior adductor scar rounded. The Sittang lineage differs from the Irrawaddy lineage in having a shorter and higher shell, more pronounced and curved lateral teeth, and a moderately strong sculpture on shell disc. The Tavoy lineage differs from the other two lineages in having an oval-shaped shell, more rounded posterior ridge, more gradual posterior slope, and distinct zigzag ridges across shell disc.

Distribution: Irrawaddy, Sittang and Tavoy River basins. In the Irrawaddy River, it is known as far north as Mya Taung and as far south as Himhada. A few records from India (e.g., Assam)14 are in need of future studies because these specimens could have been collected within the Irrawaddy Basin. The lineages from the Sittang and Tavoy River catchment areas may represent separate species- or subspecies-level taxa but requires further systematic research.

Habitat and ecology: The species seems to be rather a habitat generalist, and it is known from the mainstream of large, medium-sized and small rivers, as well as from their floodplain lakes.

Comments: Unio digitiformis Sowerby, 1868 from India is not a synonym of Indochinella pugio gen. et comb. nov59, but a separate species, the generic placement of which is unclear. Haas30 noted that the location of this form is certainly not India and that it most likely belong to the Lanceolaria Conrad, 1853.

Discussion

Taxonomic implications. Our integrative molecular and morphological approach has determined that the genus Oxynaia is polyphyletic. This result has clear implications regarding the higher-level classification of the Unionidae, the morphological characteristics of the Parreysiinae, and corroborates broader biogeographic patterns in Southeast Asia. Molecular and morphological data reject the monophyly of Oxynaia with its former constituents being recovered in phylogenetically divergent and morphologically diagnosable clades. The Oxynaia jourdyi group is unambiguously placed in the Unioninae on the basis of our molecular phylogeny and several morphological synapomorphies and is herein considered a junior synonym of Nodularia, rendering the tribe name Oxynaiini inapplicable to the Parreysiinae. This taxonomic rearrangement required the description of a new genus for the “Oxynaia” pugio group (=Indochinella gen. nov.) and a new tribe (=Indochinenlli trib. nov.) to recognize these morphologically cohesive clades of Parreysiinae.

Freshwater biogeography of Southeast Asia. Previous to this study, Oxynaia was thought to be one of the few genera distributed across much of Southeast Asia from central Myanmar to northeastern Vietnam. This distribution was thought to be unusual in that it crossed two important biogeographic barriers in Southeast Asia: (1) the Salween/Mekong river drainage divide separating the Western Indochinese freshwater mussel assemblage from the Sundaland assemblage, and (2) the Mekong/northern Vietnamese drainage divides separating the Sundaland assemblage from the East Asian fauna. However, the seemingly large distribution of Oxynaia s. lato is discovered here to be spurious and based on incorrect interpretations of common ancestry. The geographic distributions of Nodularia and Indochinella closely follow these two influential biogeographic barriers. These two biogeographic barriers divide eastern Asia into three faunistically distinct subregions (Fig. 5), each of which is briefly discussed below.

(1) Western Indochina Subregion. The drainages of the Arakan coast of Myanmar, the Irrawaddy, Pegu, Sittau,ng and Bilin river basins, and east to the Salween River and western drainages of the Kra Isthmus. The subregion currently includes members of three subfamilies (Parreysiinae, Rectidentinae and Pseudodontinae), five tribes and eight genera58. Indochinella gen. nov. is the fifth endemic unionid genus of western Indochina, together with Pseudodon Gould, 1944, Trupezoides Simpson 1900, Leoparreysia Vikhrev, Bolotov & Aksenova, 2017, and Trupezoides Bolotov, Vikhrev & Konopleva, 2017. The other genera in the region, Lamellidens Simpson, 1900, Indonaiia, and Radiatula are geographically more widespread, especially to the west into India. Radiatula is the only genus recognized to occur in the west and east of the Salween River drainage basin.

(2) Sundaland Subregion. The Mekong, Chao Phraya, Mae Klong and the drainages of the Malay Peninsula, probably corresponding to the gigantic paleo-Mekong River basin. The fauna of the Greater Sunda Islands (Sumatra, West Java, northern and western Borneo) appears similar to that of mainland Southeast Asia and may also belong to this subregion, as suggested by the molecular data for northern Borneo and by the putative connections of paleo-drainages during the Pleistocene, but further systematic research is necessary to delineate these boundaries. The Sundaland Subregion is comprised at least five subfamilies, i.e. Parreysiinae, Rectidentinae, Pseudodontinae, Goineidae, and the monotypic Modellnaiinae. A
single member of the Unioninae (i.e., *Cristaria plicata*)\(^{31,32}\) occurs in the region, although, it has likely been introduced. Two large endemic monophyletic radiations of freshwater mussels, i.e., the tribes Pilsbryoconchini and Rectidentini, were recorded in this region\(^6,7\). The highest levels of diversity of these clades occur within the Mekong River basin, with a few representatives inhabiting the Chao Phraya River, the Malay Peninsula, and the Greater Sunda Islands\(^6–9\). The Indochinellini is the only tribe of the Parreysiinae distributed in the Sundaland Subregion, whose constituents belong to a subclade *Radiatula* that appears to have significant levels of cryptic diversity (Fig. 2). Several characteristic elements of the fauna of western Indochina are lacking in Sundanese assemblage, such as the members of Lamellidentini, Leoparreysiini, and Pseudodontini.

(3) East Asian Subregion. The Red and Ca River drainage basins, and numerous coastal rivers of Vietnam comprise the East Asian Subregion, whose fauna appears to be more closely allied to the Palearctic Region than to the Oriental Region (Fig. 5). This large biogeographic subregion extends north to Japan and the

**Figure 5.** Freshwater biogeographic division of Southeast Asia based on the phylogeny and phylogeography of the Unionidae\(^5–9\). The question marks indicate areas that were tentatively assigned by us to the Sundaland Region but their placement is in need of future research. The map was created using ESRI ArcGIS 10 software (www.esri.com/arcgis); the topographic base of the map was created with Natural Earth Free Vector and Raster Map Data (www.naturalearthdata.com). (Map: Mikhail Yu. Gofarov).
Far East of Russia. This freshwater mussel fauna is entirely different from those of Western Indochina and Sundaland, and it has strong biogeographic affinities to the Pearl, Yangtze and Huang He river drainage basins. With respect to available paleontological data and phylogenetic modelling, the freshwater bivalve faunas of the Mekong and Yangtze have been developing independently since at least the early Cenozoic epoch. The East Asian Unioninae taxa such as the *Nodularia, Cristaria* Schumacher, 1817, *Sinanodonta* Modell, 1945, *Lamprotula* Simpson, 1900 and *Sinohyriopsis* Starobogatov, 1970 are the most characteristic elements of the freshwater mussel fauna of eastern Indochina at least since the Eocene, while the Rectidentinae, Parreysiinae and Pseudodontinae appear completely absent there. Based on the patterns outlined above, we suggest that the East Asian Subregion belongs to the Palearctic Region.

This biogeographic division of Southeast Asia largely corresponds with that of Graf and Cummings suggesting four freshwater biogeographic subregions, i.e. (1) Yangtze-Huang, from the Pei south to the Qiantang and Taiwan; (2) Indochina, including southern China and the Mekong west to the Salween; (3) India–Burma, from the Indus to the Irrawaddy; and (4) Sunda Islands–Philippines. However, our new scheme (Fig. 5) reveals that the Salween, Irrawaddy and Sittaung unionid faunas are close to each other and should belong to the separate Western Indochina Subregion and that the Yangtze-Huang (=East Asian) Subregion comprises the drainage basins in northern Vietnam and appears to be a part of the Palearctic Region. Additionally, we suggest that Sumatra, West Java, northern and western Borneo may belong to the Sundaland Subregion, but this preliminary hypothesis is in need of future confirmation based on an expanded molecular dataset.

Zieritz et al. distinguished two major hotspots ("epicentres") of the subfamily-level diversity and endemism of the Unionidae in Asia, i.e. (1) Southeast Asian Hotspot harboring the highest diversity of the Rectidentinae, Gonideinae (+ Pseudodontinae), Parreysiinae, and Modellnaiinae, and (2) Chinese Hotspot dominated by the Unioninae (+ Anodontini) lineages. Our biogeographic division is largely congruent with this diversity-based model, i.e., the Western Indochinese and Sundaland subregions correspond with the Chinese diversity hotspot and the East Asian Correlation with the Southeast Asian diversity hotspot.

**Methods**

**Nomenclatural acts.** The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank (http://zoobank.org), the online registration system for the ICZN. The LSID for this publication is: urn:lsid:zoobank.org:pub:C585DADC-6AB1-4692-B68A-50ABA47940A4. The electronic edition of this paper was published in a journal with an ISSN, and has been archived and is available from PubMed Central.

**Studied museum collections.** The shell lots were studied in the malacological collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH), British Museum of Natural History, London, UK (NMUK), Muséum National d’Histoire Naturelle, Paris, France (MNHN), Museo Civico di Storia Naturale di Genova, Genoa, Italy (MSNG), California Academy of Natural Sciences (CAS), North Carolina State Museum (NCSM), and Florida Museum of Natural History (UF). Additionally, we accessed the images of the types of several nominal taxa at the MUSSELp Database.

**Morphological methods.** Soft anatomy and larval characters were scored for representatives of both *Oxynaia* species groups (Table 1). These three characters were chosen as they have been previously demonstrated to be useful in diagnosing suprageneric clades of freshwater mussels. Character states were observed using a Leica M27's dissecting scope and a Leica DM LB2 compound microscope. Representative taxa relevant to the prehistoric age basins in northern Vietnam and appears to be a part of the Palearctic Region. Additionally, we suggest that Sumatra, West Java, northern and western Borneo may belong to the Sundaland Subregion, but this preliminary hypothesis is in need of future confirmation based on an expanded molecular dataset.

**Phylogenetic analyses.** We included novel *Oxynaia jourdyi* sequences in the recent phylogenetic data set of Bolotov et al. to test the monophyly of *Oxynaia*. This data set was simplified to include only one haplotype of each species, with exception of the *Oxynaia pugio* sequences (Supplementary Table 1). Additionally, we excluded several taxa that were represented only by sequences of the COI gene, but representative taxa relevant to the prehistoric age basins in northern Vietnam and appears to be a part of the Palearctic Region. Additionally, we suggest that Sumatra, West Java, northern and western Borneo may belong to the Sundaland Subregion, but this preliminary hypothesis is in need of future confirmation based on an expanded molecular dataset.

**Data availability.** The sequences used in this study are available from GenBank. Accession numbers for each specimen are presented in Supplementary Table 1.

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**Author Contributions**

I.N.B. and J.M.P. developed the concept of the study. I.V.V. coordinated field works and sampling. I.V.V., J.M.P. and E.S.K. studied the type series of the nominal taxa. I.N.B., I.V.V., E.S.K. and O.V.A. collected samples. A.V.K. designed and carried out molecular analyses, with contribution from E.S.K., M.Y.G. created the map. I.N.B. performed phylogenetic modeling. I.N.B., J.M.P. and E.S.K. wrote the paper, with input from A.V.K., I.V.V., M.Y.G., O.V.A., T.W. and S.T. All authors discussed the manuscript.

**Additional Information**

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